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COVER: Wilson's Snipe (*Gallinago delicata*). Illustration by Scott Rashid.

FRONTISPIECE. This is a reproduction of an original watercolor by George M. Sutton painted in 1952 as an illustration for the book, Georgia Birds, written by Thomas D. Burleigh and published by University of Oklahoma Press. The original paintings for the book were given in friendship to Herbert Stoddard and are part of the Stoddard Collection at Tall Timbers Research Station & Land Conservancy.

"When I made this painting, the nuthatches were not moving through the pine tops in noisy family groups, as they often do, but nesting quietly. This pair had a nest in a small hollowed-out cypress knee placed for them on a fence post. I looked a long while before finding exactly the right shortleaf pine branch for the picture. I wanted the branch, as well as the birds, to be interesting."

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COOPERATIVE BREEDING IN THE BROWN-HEADED NUTHATCH

JAMES A. COX[1,3] AND GARY L. SLATER[2]

ABSTRACT.—We monitored two color-marked populations of the Brown-headed Nuthatch (*Sitta pusilla*) for ≥5 years and collected data on survival, dispersal, territoriality, and cooperative breeding. Adults (n = 284) were sedentary, maintained long-term pair bonds, and had higher apparent annual survival (66–78%) than previously reported. Territories monitored (n = 347) contained up to five adults; the percentage of territories containing >2 adults averaged ~20% but varied widely. Most groups with >2 adults consisted of a breeding pair and a male helper related to at least one breeding adult (n = 8), but several exceptions were noted. The presence of helpers did not improve nest productivity. Apparent annual survival for females was lower than apparent survival for males in one population and may have influenced cooperative breeding. In the other population, apparent survival was similar between males and females. We suggest food resources and other environmental factors may have influenced cooperative breeding in this setting. *Received 19 January 2006. Accepted 21 July 2006.*

Cooperative breeding in the Brown-headed Nuthatch (*Sitta pusilla*) has received little attention since the behavior was first described by Norris (1958). Presumably non-breeding adult nuthatches spend large amounts of time assisting in nest construction, feeding nestlings, and defending territories (Norris 1958, Thompson 2000), but recent studies of cooperative breeding in this species are limited to two unpublished theses (Slater 1997, Thompson 2000) and a study based on 15 territories (Miller and Jones 1999).

The Brown-headed Nuthatch is a primary cavity-nesting species (McComb et al. 1986) that inhabits open pine (*Pinus* spp.) forests in the southeastern United States and the Bahamas. Populations have declined steadily throughout much of the species' range (Sauer et al. 2005) as a result of habitat loss from human development and habitat degradation through fire suppression and logging (Withgott and Smith 1998). The species also has exhibited range contraction in some regions (e.g., South Florida and Missouri), and Withgott and Smith (1998) noted that nuthatches disappeared from some areas before the endangered Red-cockaded Woodpecker (*Picoides borealis*; U.S. Department of Interior 2003) disappeared from those same areas. Accordingly, the Brown-headed Nuthatch has been designated a species of management concern in several evaluations (Hunter et al. 1993, Carter et al. 1998, U.S. Department of Interior 2002), and the Bahamian subspecies

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(*S. p. insularis*; Bond 1931) is thought to be highly imperiled (Smith and Smith 1994, Hayes et al. 2004).

Characteristics of social breeding systems have been used to develop management programs for some cooperative breeders that have undergone population declines (Walters et al. 1992, Mumme and Below 1999). Information on cooperative breeding in the Brown-headed Nuthatch could have a similar role and also broaden our understanding of social breeding systems (Boland and Cockburn 2002); however, data regarding the extent and frequency of cooperative breeding, gender of auxiliary adults, territory establishment and maintenance, and adult and natal dispersal are generally lacking (Norris 1958, Withgott and Smith 1998).

The objectives of our study were to (1) quantify and compare demographic parameters, population densities, and characteristics of cooperative breeding between two populations of Brown-headed Nuthatch in Florida, (2) develop hypotheses for factors influencing cooperative breeding in this species, and (3) consider how our information regarding cooperative breeding and other life history traits may contribute to population conservation and management.

METHODS

Study Areas.—We studied nuthatches at Tall Timbers Research Station (TTRS; 30.66° N, 84.22° W) in north Florida (2001–present) and at two sites in south Florida (1998–2003): Big Cypress National Preserve (BCNP; 26.03° N, 81.20° W) and Everglades National Park (ENP; 25.37° N, 80.59° W). TTRS encompasses 1,630 ha and is dominated by upland pine habitats consisting primarily of loblolly (*Pinus taeda*) and shortleaf pines (*P. echinata*). Dominant trees are >100 years old, and prescribed burns are conducted from March to April at two-year return intervals. Historically, upland forests at TTRS were dominated by longleaf pine (*P. palustris*), but the original forests were cleared for agriculture many decades ago (Frost 1993). In south Florida, the BCNP site is associated with an old-growth slash pine (*P. elliottii* var. *densa*) forest surrounded by a cypress (*Taxodium* sp.) mosaic. ENP contained even-aged slash pines interspersed with hardwood forests and grassy glades. Nuthatches disappeared from ENP in the early 1940s apparently as a result of extensive logging (Robertson and Kushlan 1984), and data collected here stemmed from a reintroduction program initiated in 1997. Most prescribed burns in BCNP and ENP were conducted during the early wet season (May–Jun) at 3 to 5-year return intervals.

Fieldwork and Data Analysis.—Area searches were initiated in February to locate territories and find nests. Nests were identified by worn or freshly exposed wood at cavity entrances, observing birds excavating cavities, or by finding completed nests with eggs or young. Nest locations were geographically referenced using hand-held global positioning systems. Dispersal distances, nest displacements, and territory densities were estimated using ArcView (ESRI 1998) and the straight-line distance between nest locations.

Nests were visited every 3–4 days to ascertain status and gather information on adults associated with nests. Nest height at TTRS generally was <3 m and nesting status was monitored using step ladders, flash lights, and dental mirrors. In south Florida, nest height averaged >10 m and status was monitored using behavioral observations (typically <30 min/visit). A breeding attempt was defined as the presence of eggs or behavioral cues indicating nesting was underway (used for tall nests).

Nestlings were banded 13–16 days after hatching at TTRS by removing the front of nesting cavities using a small saw. The cavity face was secured after banding using wood putty, staples, and masking tape. A single federal band was affixed to nestlings. All adults were color banded. The height of nests in South Florida precluded banding of young, and data on dispersal for second-year (SY) birds and nestlings stemmed exclusively from the TTRS population. We compared productivity between pairs and cooperative groups within populations using (1) the number of nestlings banded per nest (TTRS) and (2) the number of fledglings counted on at least two visits (south Florida) less than two weeks after young left the nest.

Most adults were captured using mist nets placed near nests, but a few individuals were lured into mist nets using recorded vocalizations of nuthatches or Eastern Screech-owl

TABLE 1. Data for color-marked populations of the Brown-headed Nuthatch in Florida.

Study area	North Florida	South Florida
Study length (years)	5	6
Territories monitored	152	195
Territories with helpers (%)[a]	22.7 ± 11.4	17.3 ± 16.1
Maximum group size	5	4
Territories with nests (%)[a]	85.2 ± 9.2	83.2 ± 22.4
Adults banded	148	136
Females	66	57
Males	62	57
Unknown	20	22
Nestlings banded	246	
SY[b] in natal territories	8	
SY[b] Dispersed	8	
Apparent annual survival[c]		
Females (%)[a]	66.1 ± 5.3	68.7 ± 13.1
Males (%)[a]	77.8 ± 4.7	69.3 ± 15.8

[a] Mean ± SD.
[b] Second Year (SY) individuals banded as nestlings and recaptured the next breeding season.
[c] Estimates obtained from Program MARK (White and Burnham 1999).

(*Otus asio*). Gender was assigned based on the presence (female) or absence (male) of a brood patch on breeding birds, behavioral observations of color-banded birds (e.g., copulation), and presence of a cloacal protuberance (male; Norris 1958, Pyle 1997). Wing length was used to assign gender for some SY helpers captured at TTRS if other traits were equivocal. Wing length averaged 2.5 mm longer for males than females among individuals whose gender was assigned using other criteria (t-test = −9.657, $P < 0.01$; all measurements by JAC). Wing length also appeared to vary with age, so gender of some SY birds was assigned only when observed in subsequent breeding seasons.

Adults were fitted with three plastic color bands and an aluminum federal band (two bands per leg; federal permits 22446 [JAC] and 22932 [GLS], state permit WB04060a). Plastic bands were sealed using acetone. Except where noted, results were based on color-banded individuals and banded nestlings recaptured as adults.

The size of breeding groups was estimated by observing the number of adults engaged in nesting activities (i.e., cavity excavation, nest building, or providing food for young or incubating females) on >2 occasions during the breeding season. Recorded nuthatch vocalizations played near nests were used to solicit territorial responses during some visits. Vocalizations, copulation, incubation, and dominance (Norris 1958) were used to categorize breeding status either as breeding adult or an auxiliary helper; however, individuals described as helpers may have been breeders (Richardson et al. 2001).

Apparent adult survival was estimated with Program MARK (White and Burnham 1999) using observations of color-banded adults during subsequent breeding seasons (Feb–Jul). Data for north and south Florida were analyzed separately because of differences in years of study and number of populations monitored. Global models that included variation in apparent survival and recapture probabilities based on gender, site (south Florida only), and year were considered initially. Nested models for north and south Florida were evaluated using information-theoretic methods (Anderson et al. 2000).

RESULTS

Group Size and Frequency; Gender and Influence of Helpers.—The largest breeding group contained 5 adults, but most (>70%) groups with >2 adults contained 3 adults. The frequency of territories with >2 adults ranged from 10 to 32% and appeared to be more variable in south Florida (CV = 0.93) than at TTRS (CV = 0.50; Table 1). Most helpers were SY males that assisted at the nest of at least one parent (n = 8), but we also found males that assisted parents for at least 3 years (n = 2). A female helper (gender based on observations in later years) was recorded in south Florida and assisted with incubation.

The presence of helpers had no apparent effect on the number of young produced. In north Florida, we banded an average of 4.35 (SD = 1.11) nestlings in nests tended by >2 adults (n = 34) and 4.16 (SD = 1.45) nestlings in nests tended by pairs (n = 117; t-test = −0.534; P = 0.541). In south Florida, territories with helpers (n = 17) averaged 2.94 fledglings per successful nest (SD = 1.19), while territories consisting of pairs (n = 139) averaged 2.90 fledglings per successful nest (SD = 1.07; t-test = −0.147; P = 0.883). However, dead nestlings were found buried in some nests tended by pairs (n = 5) and suggested brood reduction occurred. Body mass differences among nest mates also frequently exceeded 1.5 g (~20% nestling mass in the later stages of development).

We observed six cases where adult males provided assistance at neighboring nests following the failure of their nests (i.e., facultative helping). Two males provided assistance at a neighboring nest 3–5 days after they lost their nests (and presumably their mates). The remaining four cases involved breeding males that assisted other nests in subsequent breeding seasons.

Variation in Apparent Survival and Nesting Attempts.—The most parsimonious model selected from Program MARK for south Florida included variation in apparent survival by site (BCNP vs. ENP) but held apparent survival and recapture probabilities (P = 1.0) constant by gender and year. The most parsimonious model for TTRS incorporated variation in apparent survival due to gender but held recapture probabilities (P = 0.93) and survival rates within gender constant among years. Apparent annual survival was >65% for both populations but appeared to be more variable in south Florida (CV > 0.15; Table 1). Males in north Florida had the highest apparent survival (Table 1), while females in north Florida had the lowest apparent survival (Table 1). We also observed new sources of adult mortality: five females tending nests at TTRS were killed either by red ratsnakes (*Elaphe guttata*) or small mammals.

Breeding attempts were observed in >80% of the territories monitored each year with considerable variation among study sites and years (range = 33–100%). South Florida study sites exhibited greater variation in the proportion of active territories, and annual nesting attempts were <65% in some years (Table 1). In south Florida, group size was identified in 27 of 42 territories without breeding attempts. The majority of groups consisted of pairs (n = 18), followed by single birds (likely males; n = 6), and groups of three individuals (n = 3). In north Florida, territories without observed nesting attempts appeared to consist of single males (n = 3) or groups of males (n = 2 based on color-banded individuals) that either failed to attract mates or lost mates before eggs were laid.

The primary sources of nest failures at TTRS were depredation (24%) and cavities burned by prescribed fires (21%). In south Florida, most nest failures (37%) appeared to stem from nest depredation based on the cavity damage observed. We also recorded a new egg predator at two nests: broad-headed skink (*Eumeces laticeps*).

Pair-bond and Site Fidelity.—Pair bonds extending over several years were common, and approximately 50% of the territories consisted of individuals paired the previous year. Pair bonds became established at almost any time of the year. Two juveniles banded in the same area in July were paired as breeders the following breeding season. In contrast, a male that completed a cavity in mid-March did not attract a mate until mid-April. We also observed unpaired males (n = 5) excavating cavities and maintaining territories throughout the breeding season.

Breeding pairs frequently excavated their nests within 100 m of nests excavated the previous year. Some breeding groups (n = 5) excavated nesting cavities in the same snag for ≥2 years. Site fidelity also was evident when individuals remained in their territories following the apparent loss of parents (n = 2) or mates (n = 7). Most individuals that retained territories successfully attracted new mates in subsequent breeding seasons, but more complex scenarios also occurred. In one case, two male siblings that hatched a year apart (the older sibling was a helper when the younger sibling was a nestling) remained in their natal territory following disappearance of their parents. These males attracted an unbanded female and initiated a nest in the territory held by their parents the following breeding season. Two years later, the younger sibling was observed assisting at a neighboring territory while the older sibling had disappeared.

Territory Proximity and Dispersal.—Nuthatch densities were higher in north Florida than in south Florida. The distances between nearest neighboring nests was significantly lower at TTRS (mean = 198.5 m, SD = 90.7) than in south Florida (mean = 394.9 m, SD = 242.8; *t*-test = 12.86, $P < 0.001$). Nearest neighbor distances at TTRS also generally were more consistent from year to year. Average distances at TTRS ranged from 199 to 216 m annually (CV = 0.04), while average distances in south Florida ranged from 370 to 550 m (CV = 0.169). Nearest neighbor distances suggest densities of 0.33 territories/ha at TTRS and 0.08 territories/ha in south Florida.

Most observed dispersal events spanned short distances. Seven SY males established territories or assisted at territories within 300 m of the territory held by their parents (i.e., generally the nearest neighboring nest to the natal territory). In two cases, the SY males were nest mates that each attracted unbanded females and initiated nesting attempts within 100 m of their natal nest. In a third case, two SY siblings were associated with a single female and initiated a nest within 300 m of their natal nest. In a fourth case, a SY male was captured assisting at a territory adjacent to his natal territory. The territory was held by a male banded the previous breeding season, while the father of the SY male was engaged in a nesting attempt <150 m away and assisted by a nest mate of the SY male at the neighboring nest. Two males also established territories next to territories of the breeding adults they assisted during a previous breeding season.

Four SY males were recaptured ≥2 territories from natal territories. Dispersal averaged 1,358 m for males dispersing ≥2 territories. The limited data primarily demonstrate that some males disperse and attempt to breed (successfully [$n = 2$]) in their first year, while others stay and help. Dispersal of older individuals (after their SY) ≥2 territories also occurred infrequently ($n = 3$). Two breeding females relocated 586 and 1,020 m, respectively, while a male associated with a four-adult breeding group in 2003 became a breeder in a territory 2,080 m away in 2004. There were no recaptures of SY females at TTRS.

DISCUSSION

The extent of cooperative breeding we observed (~20%) is similar to that reported in Georgia (Norris 1958), north Florida (Miller and Jones 1999), and Texas (Thompson 2000) and demonstrates cooperative breeding occurs consistently throughout the range of this species. Although the behavior is widespread, Ligon and Burt (2004) noted the potential benefits and constraints that favor the behavior have not been identified. Our data suggest potential direct benefits include acquisition of the territory of a parent or neighbor (Woolfenden and Fitzpatrick 1984, Walters 1990) as well as assistance provided by offspring that are helped (Hannon et al. 1985). Helpers also may benefit through other means that we did not assess, including extra-pair fertilizations, egg-dumping (Richardson et al. 2001), and increased survival or productivity.

Arnold and Owens (1998) reported high annual survival was an important factor favoring the expression of cooperative breeding in many avian lineages. Our estimate for annual survival for the Brown-headed Nuthatch (66–78%) is high for a small passerine (Martin 1995) and markedly higher than the estimate of 54% reported by Norris (1958). We also found gender-based differences in survival in north Florida and believe this influenced cooperative breeding. Skutch (1961) originally suggested a shortage of female nuthatches might constrain breeding opportunities for males (based on sex ratios reported in Norris 1958), and we found additional support for this hypothesis in the discovery ($n = 5$) of breeding females consumed by ratsnakes and small mammals in nesting cavities.

Lower survival among females may be related to the strong nest attentiveness exhibited during incubation and brooding coupled with the low height (<3 m) of cavities used at TTRS (and elsewhere; McNair 1984). Females rarely flushed when nests were inspected at TTRS, and we suspect this behavior reduced egg depredation (Dornak et al. 2004) by small lizards or nest usurpation by cavity competitors (e.g., Carolina Chickadee, *Poecile carolinensis*). This behavior leads to higher predation risks for females (Martin and Li 1992), especially later during the breeding season when warmer ambient temperatures lead to increased snake activity (Neal et al. 1993, Weatherhead and Blouin-Demers 2004).

In contrast, the absence of gender-based survival differences in south Florida suggests factors such as food resources (Koenig and Stacey 1990) or habitat features (Walters 1990) may constrain breeding opportunities in this region. This hypothesis is consistent with our data suggesting that habitat quality is lower in south Florida (e.g., lower territory densities, greater variation in annual breeding effort, and greater variation in adult survival; Table 1). Nest productivity also appeared to be lower in south Florida than at TTRS and elsewhere (Morris 1982, Miller and Jones 1999, Thompson 2000). McNair (1984) also noted reduced clutch sizes for nuthatches in south Florida and suggested the reductions stemmed from environmental factors.

Nuthatches in south Florida select nest territories with a greater proportion of large pines (Slater 1997), and the density and diversity of large pine trees might affect food resources and habitat quality (Koenig and Haydock 1999). Large pines produce proportionally more seeds than smaller pines (W. J. Platt, pers. comm.), and nuthatches cache and rely heavily upon pine seeds during the winter (Yaukey 1995). We did not measure pine seed production, but we suspect it is more variable in south Florida where only one species of pine occurs (slash pine). TTRS supports four species, including two consistent seed-producers (loblolly and short-leaf pines; Cain and Shelton 2001). Large pines also have greater surface area, providing more foraging space.

Helpers appeared to be closely related to breeders, and alloparental care may include indirect benefits (Brown 1978). Even for situations where individuals provided assistance at neighboring nests, the short dispersal distances we recorded suggested neighbors often were closely related. Three adjacent territories monitored in 2004 consisted of (1) a father, (2) a son born in 2002, and (3) a son born in 2003. In addition, the father was assisted in 2004 by a male offspring born in 2003. We observed six other cases where adjacent territories were held by siblings or parent-offspring combinations. Helpers also may lighten feeding responsibilities for females and enable them to initiate second clutches (Thompson 2000). Helpers also may serve as sentinels (McGowan and Woolfenden 1989) and decrease female (and in most cases maternal) susceptibility to predators.

Cooperative breeding in the Brown-headed Nuthatch is similar to Pygmy Nuthatch (*S. pygmae*) behavior and suggests this trait was present in a shared ancestor (Ligon and Burt 2004). Helping behavior is observed in about 15–30% of the annual territories of both species (Norris 1958, Miller and Jones 1999, Kingery and Ghalambor 2001) and less frequently reaches frequencies as high as 40% (Slater 1997, Miller and Jones 1999, Kingery and Ghalambor 2001). Facultative helping occurs infrequently (Sydeman 1991) and, while breeding groups may include up to five adults, they more typically contain either two or three adults (Sydeman et al. 1988). Cooperative behavior in the Pygmy Nuthatch has been linked both to skewed sex ratios (Norris 1958, Skutch 1961) and environmental features (Sydeman et al. 1988).

The life-history characteristics we documented in association with cooperative breeding suggest that management of small, isolated populations of Brown-headed Nuthatches deserves special attention. This species is relatively sedentary and appears to disperse short distances. Accordingly, it is unlikely to re-colonize isolated areas should populations disappear (Walters et al. 2004). This phenomenon has already occurred in south Florida (Robertson and Kushlan 1984) and other areas where the species' range has contracted. Management should focus on retention of mature, seed-bearing pine trees, particularly in situations where pine basal area is low and only 1–2 species of pines exist. Retaining sufficient snag resources also should alleviate competition for nesting sites (McComb et al. 1986) and reduce nest depredation (Li and Martin 1991). Timing of prescribed burns also deserves attention where small, isolated populations exist. Frequent prescribed burning is essential for maintaining suitable habitat conditions (Engstrom et al. 1984), but burns conducted during the nesting season destroy nests and shift re-nesting to periods with warmer ambient temperatures.

Our study suggests that cooperative breeding in the Brown-headed Nuthatch is a fluid behavior that should be amenable to experimental manipulation. For example, female survival in north Florida may be improved by protecting nesting cavities from predators (e.g., Withgott et al. 1995). This treatment should lead to fewer breeding groups consisting of >2 adults (unless the habitat becomes saturated). Supplemental food (e.g., Egan and Brittingham 1994, Yaukey 1995) could be provided in south Florida to learn if group size increases in territories with better food resources (Koenig and Stacey 1990).

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AGE-SPECIFIC STOPOVER ECOLOGY OF BLACK BRANT AT HUMBOLDT BAY, CALIFORNIA

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ABSTRACT.—We analyzed capture-mark-recapture (CMR) data from 1,061 Black Brant (*Branta bernicla nigricans*) using Humboldt Bay, California, during northward migration (Jan–May), 2000–2001. We estimated immigration and emigration rates, and calculated stopover duration (length of stay), volume (total number of birds using the Bay), and chronology (time frame of the migration at this site). Migration of Brant through Humboldt Bay began in late December and ended in mid-May with peak numbers occurring in mid-March (i.e., 13% of the entire flyway population). Median age of newly arrived birds was highest in the first half of February. Immigration probability was nearly constant, but emigration probability increased through time, indicating a seasonally progressive migratory state. Mean (±SE) stopover duration from all birds for January–April at Humboldt Bay was 26 ± 2 days. Stopover duration was inversely related to bird age due to age-specific emigration probabilities; older birds arrived sooner and stayed for less time than younger birds. Estimates of stopover duration from concurrent radiotelemetry of 12 birds were consistent with CMR model selection-derived estimates. Humboldt Bay was visited by approximately 28% of the Pacific Flyway Black Brant population in 2000 and 58% in 2001. Estimates derived from this technique offer statutory authorities improved information upon which to base management action along migratory pathways. *Received 5 December 2005. Accepted 24 July 2006.*

Annual movements of migratory birds cover vast distances. Understanding behavior at stopover sites—where migrants accumulate or replenish energy stores en route (Alisauskas and Ankney 1992, Prop et al. 2003)—is crucial to understanding reproductive success, life history, and population dynamics (Owen and Black 1991, Ebbinge and Spaans 1995, Yong et al. 1998). Stopover behavior is primarily shaped by time, energy, and predation forces (Alerstam and Lindstrom 1990), and affects migration strategy (Alerstam and Hedenstrom 1998). Stopover behavior also has conservation implications because these sites function as geographic bottlenecks where large portions of the population congregate (Myers 1983), sometimes differentially by age (Yong et al. 1998, Restani 2000). Under the Ramsar Convention (Ramsar Convention Bureau 1988), any staging area that hosts >1% of one or more waterbird populations is considered of international importance and should be safeguarded. Thompson's (1993) theoretical model to describe shorebird migration provides an excellent framework for examining migratory behavior of all birds from the perspective of the stopover site. The key parameters in Thompson's (1993) model are immigration and emigration probabilities, which can be accurately estimated with capture-mark-recapture (CMR) models (Schaub et al. 2001). Stopover duration (called residence time in Routledge et al. 1999) can be calculated from immigration and emigration rates (Pradel et al. 1997b, Schaub et al. 2001). Stopover duration, the total time an animal spends in a defined area between migratory bouts, is an important component of optimum migration models (Weber and Houston 1997). By combining emigration probabilities with periodic census data, volume or superpopulation (the total number of birds that passed through the area during migration) can be computed (Frederiksen et al. 2001, Schaub et al. 2001).

We used CMR data from Black Brant (*Branta bernicla nigricans*) migrating through

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Humboldt Bay, California, during winter and spring (Jan–May, 2000–2001), and program MARK (White and Burnham 1999) to model and estimate periodic immigration, emigration, and recapture probabilities. We used MARK's ability to include individual covariates to examine how bird age affected immigration and emigration probabilities. We computed stopover duration, volume, and proportion of transients (birds observed only once), and described overall migration chronology and age-specific chronology. We validated our estimates of stopover duration computed from CMR data with simultaneously collected radiotelemetry data.

HYPOTHESES

Age-specific Stopover and Chronology.—Gauthreaux (1978) reported that dominance is the primary underlying force behind intraspecific behavioral variation. Geese increase their migratory experience, dominance, and reproductive investment as they age (Rockwell et al. 1983, Black and Owen 1989, Stearns 1992). Peak reproduction for geese is from ages 6 to14 years (Black and Owen 1995; Sedinger et al. 1998, 2001), and reproductive success contributes to increased dominance (Black and Owen 1989). Reproductive success in geese has also been found to depend upon individuals arriving at the farthest north stopover area early, and maximizing time spent there (Madsen 2001). Palmer (1976) suggested differential chronology of spring migrants by age with paired breeders generally among the first migrants. Humboldt Bay is a Brant stopover area in the southern to middle portion of their range. We expected older (more experienced and dominant) birds would make most efficient use of resources available by arriving earlier than young birds, and have shorter stopover duration before moving to staging sites closer to breeding areas.

Volume.—Humboldt Bay is believed to be the most important spring staging area for Brant in California (Pacific Flyway Subcommittee on Pacific Brant 1992), and one of the most important in the entire flyway (Humboldt Bay National Wildlife Refuge, U.S. Fish and Wildlife Service, unpubl. data). We expected our estimates of volume to confirm that Humboldt Bay was used by a large proportion of the population.

Seasonal Progression and Transience.—Previous studies of stopover ecology have detected a seasonally progressive trend in emigration probability (Pradel et al. 1997b) and an excess of animals that are not observed again after their first observation (Pradel et al. 1997a, 1997b; Reed et al. 1998a). We incorporated these possibilities and tailored the analyses to include tests of transience and temporal trends in emigration probability.

Techniques.—We computed two CMR modeling-derived estimates of stopover duration (Reed et al. 1998a, Schaub et al. 2001) and used radiotelemetry-derived estimates to validate each method.

METHODS

Capture-Recapture Data Collection

We conducted this study on Humboldt Bay National Wildlife Refuge (HBNWR), on the coast of northern California (40° 48′ N, 124° 07′ W). Humboldt Bay is a 62.4-km^2 estuary (Barnhart et al. 1992) with 1,044 ha of eelgrass (*Zostera marina*) in discrete beds interlaced with a dendritic network of channels (Moore et al. 2004). Black Brant feed almost exclusively on eelgrass during the non-breeding season (Derksen and Ward 1993). South Humboldt Bay (South Bay) contains 70% of the eelgrass beds in Humboldt Bay, and supports 78–94% of Humboldt Bay Brant use each year (Humboldt Bay National Wildlife Refuge, U.S. Fish and Wildlife Service, unpubl. data). Humboldt Bay is the only large estuary containing substantial eelgrass beds (>300 ha) for 350 km to the south and 600 km to the north along the coast (Moore et al. 2004), making it an insular study area with little potential for regional foraging movements. South Spit, the sandy peninsula separating South Bay from the Pacific Ocean, has one large, and many small intertidal sand bars along its eastern shoreline that are used by Black Brant as the tide ebbs to rest, preen, and ingest grit.

Annually, samples of all ages of individual Black Brant are marked with uniquely coded tarsal bands at major breeding and molting locations in western and northern Alaska, Russia, and the Northwest Territories (Sedinger et al. 1993, Ward et al. 1993, Bollinger and Derksen 1996). In fall, most Black Brant migrate south to overwinter on coastal lagoons of Baja California, Mexico (Reed et al. 1998b). During all daylight ebbing tides from 1 January to 1 May in 2000 and 2001, we used 60–120× spotting scopes to read tarsal bands of Brant on Humboldt Bay sand bars. Successful reading of a band constituted an encounter for each individual, and the entire record of encounters constituted the individual's encounter history. In terms of capture-recapture data, the first observation of a marked bird is considered its capture, and subsequent observations are recaptures. Observed birds were classified by gender, and real (banded as a gosling or yearling) or minimum (banded after second year) age from information in banding records (Sedinger et al. 1993).

In July 1999, 45 Brant were fitted with radio transmitters on the Yukon-Kuskokwim Delta, Alaska (D. H. Ward, pers. comm.). Transmitters consisted of a crystal and battery encased in epoxy with a 20-cm whip antenna, and were surgically implanted. Thirty-four of these radio-marked birds were relocated alive with operational transmitters in Baja California, Mexico in winter 1999–2000 (D. H. Ward, pers. obs.), prior to northward migration. During 2000, we monitored all 34 radio frequencies daily from two elevated (50–75 m) locations (Bell Hill and Table Bluff) overlooking South Bay to collect presence-absence data for each radio-marked bird. Receivers at Bell Hill and Table Bluff identified transmitters at distances spanning the farthest extent of South Bay from the receiver sites (5 km and 8 km, respectively). Thus, radio-marked birds present on the Bay should have been detectable at all times.

Capture Recapture Analysis

We used encounter histories to model and estimate recapture, emigration (the complement of residence) and immigration (the complement of seniority) probabilities using program MARK 1.8 (White and Burnham 1999) following methods described by Schaub et al. (2001). The three parameters we modeled and estimated were (1) recapture (p_i), the probability that a previously observed bird is observed at time *i*, given that it is present in the study area at time *i*; (2) residence (ϕ_i), the probability that a bird in the study area at time *i* remains in the study area until time $i + 1$; and (3) seniority (γ_i), the probability that a bird present at time *i*, was present in the study area at time $i - 1$.

Recapture.—The superiority of CMR modeling methods of analyzing bird band data lies in the estimation of recapture probability (p). Residence and seniority estimates are otherwise biased low because they do not account for the proportion of banded birds that are alive and present, but not seen. We were able to more accurately estimate arrival and departure probabilities by modeling recapture probability for residence and seniority.

Emigration.—During spring, emigration from the study area is much greater than natural mortality. The parameter ϕ_i, properly defined as apparent survival, is the product of true survival and residence probability, defined as the probability of remaining in the study area between times *i* and $i + 1$. True survival of Brant was previously estimated for winter (1 Jan–1 Mar) as 1.00 and early spring (1 Mar–15 Apr) as 0.988 (Ward et al. 1997). We assumed zero mortality during the entire study period (1 Jan–1 May), making apparent survival equal to residence probability. Thus, in our case, ϕ_i can be subtracted directly from 1 to calculate emigration probability, the probability of an individual leaving the study area between times *i* and $i + 1$.

Immigration.—Pradel (1996) developed a CMR model parameterization that produces estimates of γ_i, called the seniority probability, defined as the probability of an animal having been in the population previous to the first capture. During spring, the occurrence of all new Brant in the study area is due to immigration (birth rate = zero). Thus, the probability of immigration into the study area between times *i* and $i + 1$ is $1 - \gamma_i$.

Pooling.—Due to weather-restricted visibility, Brant leg bands were not observable on some days. These gaps in the daily capture histories made daily estimates of immigration and emigration probabilities impossible. Thus, for model selection we used the common technique of pooling the data (Pradel et al. 1997b, Reed et al. 1998a). Pooling violates model assumptions of independent observations and instantaneous sampling periods, and can lead to biased parameter estimates (Hargrove and Borland 1994), but was necessary in this study to permit modeling (Schaub et al. 2001). Different pooling intervals were tried for each year's data. The intervals ultimately chosen were the shortest periods that met two criteria: (1) global models successfully converged, and (2) global models passed goodness of fit criteria (data deviance ranked <90/100 simulated deviances). Data were pooled into 7- and 5-day periods for 2000 and 2001, respectively. The number of observation periods with no data was one in 2000 and three in 2001; no gaps were consecutive. Gaps were accounted for by changing the time interval between observations from one to two in program MARK. The pooling interval differed by year, precluding direct between-year comparisons, but minimized biases within years from excessive pooling. Tests of true age effects used a subset of the data that was pooled into 14-day periods based on convergence and goodness of fit criteria. Only year 2001 data were used for true age model selection because known age data were too sparse in 2000 to permit modeling. There were no data gaps in the true age data.

True Age.—We tested a subset of known-age birds for differences in immigration and emigration due to true age (years since hatching). These models were designed with bird age as a standardized, continuous, individual covariate of the parameter of interest. The covariate was considered to have a significant effect on the parameter if the model including the age covariate had a lower $QAIC_c$ value than the model without it. The sign of the beta coefficient for age in ϕ and γ indicates the relationship between emigration and immigration to age. In each observation period with sample size >5 of newly arrived known-age birds, median age and proportion of birds >5 years old were calculated to investigate age differences in migration chronology.

Model Subscripts.—We used notation similar to that suggested by Lebreton et al. (1992) to designate the models. We designated a fully time-dependent parameter with a "*t*" subscript, and a constant parameter with a "*c*" subscript for residence (ϕ), seniority (γ), and recapture (p) probabilities. Parameters were also modeled as linear and quadratic trends through time, denoted with subscripts "T" and "T^2", respectively. When true bird age was included as an individual covariate of a parameter we used the subscript "*age.*" The subscript "*e#*" was used to control for extreme parameter heterogeneity between the initial observation and subsequent observations. The "*e*" subscript denoted encounter class structure, and the # denoted how many encounter classes were present. Encounter class structure was included in residence, but is not possible to model in the seniority probability.

Transience.—The RELEASE goodness-of-fit procedure in program MARK showed that residence probability of newly observed and previously observed individuals differed, indicating a large portion of the newly observed individuals was present for only one observation period. Transients (individuals with a zero probability of residence after their initial observation) are a likely explanation of this disparity in our data (Pradel et al. 1997a). Presence of large numbers of transients required encounter class structure ($\phi_{e\#}$) to be added to residence models to account for this extreme form of heterogeneity. In these model structures, the first # encounter classes are a mixture of residents and transients, with subsequent encounter classes made up solely of residents. Thus, the notation "*e2*" would denote two encounter classes—the first a mixture of transients and residents, the second composed entirely of residents.

Model Selection.—Model selection was based on Akaike's information criterion corrected for small sample size (AIC_c; Akaike 1974, Burnham and Anderson 1998). All models used the logit link function. We assessed goodness-of-fit (GOF) for the most general model in each set by the bootstrapping method included in program MARK. We calculated the deviances from 100 simulations of data that are not over-dispersed. We accepted a general model if its deviance ranked <90 of the 100 rank-ordered deviances simulated. The ratio of the data's deviance to the mean deviance from the bootstrapping simulations was computed as the variance inflation factor ($\hat{c}$) for each data set. The bootstrapping method cannot be directly applied to immigration models, so the variance inflation factor from the emigration model for a given data set was applied to both model selection procedures.

Individual covariates cannot be included in bootstrapping simulations. When $\hat{c}$ was applied to a data set, AIC_c values became quasi-likelihood AIC_c ($QAIC_c$) values. Parameter standard errors were multiplied by the square root of $\hat{c}$ to adjust for lack of fit. Once the fit of the general model was assessed, reduced models were fitted to the data. The most parsimonious models were selected from among the pool using $QAIC_c$. The model with the lowest $QAIC_c$ value was considered the best or most parsimonious model. Akaike weights (Burnham and Anderson 1998) were computed to denote relative strength of evidence supporting each model.

The general emigration model was first reduced by finding the optimum number of encounter classes for ϕ with time dependence in each class. Once the best time-dependent reduced encounter class model was found for ϕ (two encounter classes), we ranked all combinations of c, t, T, and T^2 in each encounter class of ϕ (including additive models; i.e., $e2 + T$) and all combinations of c, t, T, and T^2 in p for a total model set of 67 emigration models. For immigration, we ranked all combinations of c, t, T, and T^2 in γ and p for a total of 16 immigration models.

For true age, we first found the optimum number of encounter classes in ϕ (2), and then simplified the general model by reducing p, then ϕ or γ to keep the number of total models tested reasonable in light of the reduced data set (Lebreton et al. 1992). We reduced p by ranking all combinations of *age*, c, t, and T in p including additive and multiplicative relationships of *age* with temporal terms (e.g., $age + T$ and $age \times T$) while holding ϕ or γ in its most general form. Then, we held p in its most parsimonious form while reducing ϕ or γ by ranking all combinations of *age*, c, t, and T including additive and multiplicative relationships of *age* with temporal terms for a total of 24 emigration and 16 immigration models.

Several models often appear equally plausible in the final set, with $\Delta QAIC_c$ values near zero and $QAIC_c$ weights comparable to the best model. Model averaging was used to create parameter estimates to account for apparent model selection uncertainty (Burnham and Anderson 1998). Model averaging uses AIC_c weights to calculate the weighted average of each real parameter across all models with AIC_c weights greater than zero.

Stopover Duration

Methods for computing stopover duration are dependant upon the true distribution of stopover durations in the population (Efford 2005). We used model-averaged parameter estimates of ϕ_i and γ_i in Schaub et al.'s (2001) equation to calculate stopover duration (D_i). D_i is defined as the mean stopover duration in days for birds present in time i and assumes most birds spend approximately the same time at the stopover site. We made a second estimate for stopover duration using only ϕ_i (Reed et al. 1998a), that assumed a Poisson distribution in stopover durations. Confidence intervals of stopover duration were calculated using a non-parametric bootstrap procedure (Schaub et al. 2001).

$$
\begin{aligned}
D_i = {} & \sum_{k=i}^{n} \left(\prod_{j=i}^{k-1} \phi_j \right) \left(-\frac{1 - \phi_k}{\ln \phi_k} \right) + \left(\prod_{j=i}^{n} \phi_j \right) \frac{-1}{\ln \phi_{n+1}} \\
& + \sum_{k=n-i+1}^{n} \left(\prod_{j=i}^{k-1} \gamma_j \right) \left(-\frac{1 - \gamma_k}{\ln \gamma_k} \right) \\
& + \left(\prod_{j=n-i+1}^{n} \gamma_j \right) \frac{-1}{\ln \gamma_{n+1}} \gamma_j
\end{aligned}
$$

Mean stopover duration for radio-marked Brant was calculated directly from detection data because fate of all radio-marked animals was assumed known with certainty ($p = 1$). Mean stopover duration of radio-marked Brant was compared with mean stopover duration of banded Brant computed from the two CMR-derived estimates by GLM using a Poisson distribution and log link function (clustered by date of arrival). Radio-marked birds were present at the study site for only a portion of the 2000 band observation period, and the test compared stopover duration estimates only for the time interval when radio-marked birds were present.

Volume

The number of Brant present on South Humboldt Bay was measured by census every week in 2000, and every fortnight in 2001. Censuses were conducted hourly using 60× spotting scopes from Bell Hill, Table Bluff, and South Spit during the 4 hrs before and after daylight low tides; mean counts were

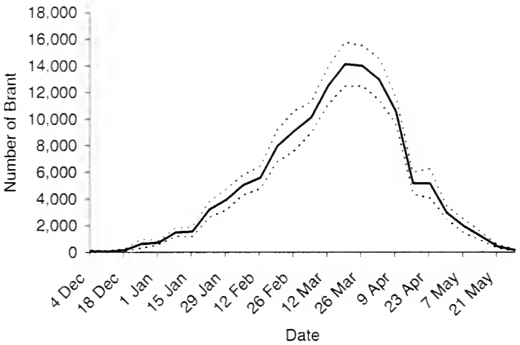

FIG. 1. Ten-year mean (1990–99) number of Black Brant present on Humboldt Bay, California, by date, during northward migration. Dotted lines are mean ± 1 SE.

then computed. The mean count data were combined with emigration rates to calculate volume and the total number of birds using the site during each migratory season using the Frederiksen et al. (2001) estimator. For estimates of emigration for time intervals between censuses, the number of Brant present on South Bay was interpolated by fitting a line between the two censuses that bracketed the missing time. Volume estimates for South Bay were divided by 0.83 (mean proportion of Humboldt Bay Brant use occurring on South Bay from 1992 to 2000) to estimate volume for all of Humboldt Bay.

RESULTS

We had 452 observations of 320 uniquely banded individuals between January and April 2000, and 1,466 observations of 741 individuals between January and April 2001. Numbers of Brant on Humboldt Bay ($\geq$1,000) sufficient to obtain adequate sample sizes of band readings appeared at the end of December, and ended in mid May, with peak numbers ($\sim$17,000) in mid-March. This pattern of migration chronology was typical for Humboldt Bay Brant use over the past decade (Fig. 1).

Model Selection 2000.—The initial model considered in estimating emigration ($1 - \phi_i$) for all Brant using Humboldt Bay in winter and spring 2000 was that with fully interactive time- and transient encounter class-dependent residence and time-dependent recapture probabilities $\{\phi_{e12\cdot t}, p_t\}$. Bootstrapping indicated this model was an adequate general model to begin selection (deviance rank = 84/100). Although GOF was acceptable, a variance inflation factor of $\hat{c}$ = 1.286 was used as a measure of conservatism. The best residence model selected by QAIC$_c$ was $\{\phi_T, p_T\}$ (Table 1). Residence and recapture in this model followed a linear trend through time. QAIC$_c$ weights showed several competing models with appreciable strength of evidence (Table 1) that contributed information (such as transient en-

TABLE 1. Model selection results (top 95% model set by weight) for Black Brant during January–May 2000 at Humboldt Bay, California with variance inflation factor ĉ = 1.286, ϕ = residence probability, γ = seniority probability, and p = recapture probability. Model with zero ΔQAIC$_c$ is considered the most parsimonious. QAIC$_c$ weight is the relative strength of evidence supporting a given model.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Parameters	QDeviance
Emigration					
$\{\phi_T, p_T\}$[a]	606.72	0.00	0.26	4	158.77
$\{\phi_{e2+T}, p_c\}$	607.82	1.10	0.15	4	159.87
$\{\phi_{e2+T}, p_T\}$	607.91	1.19	0.14	5	157.91
$\{\phi_c, p_T\}$	608.95	2.23	0.09	3	163.05
$\{\phi_T, p_t\}$	609.06	2.34	0.08	13	142.22
$\{\phi_{e2*T}, p_T\}$	609.13	2.41	0.08	6	157.06
$\{\phi_T, p_c\}$	609.34	2.62	0.07	3	163.44
$\{\phi_c, p_t\}$	609.68	2.97	0.06	12	144.99
$\{\phi_{e2}, p_T\}$	610.95	4.24	0.03	4	163.01
Immigration					
$\{\gamma_c, p_T\}$	617.64	0.00	0.47	3	171.74
$\{\gamma_c, p_t\}$	619.22	1.58	0.21	11	156.71
$\{\gamma_T, p_T\}$	619.27	1.63	0.21	4	171.33
$\{\gamma_T, p_t\}$	621.33	3.69	0.07	12	156.70

[a] Subscripts: t = time dependence (each week differs), c = constant through time, T = logit-linear trend through time, and $e2$ = two encounter classes.

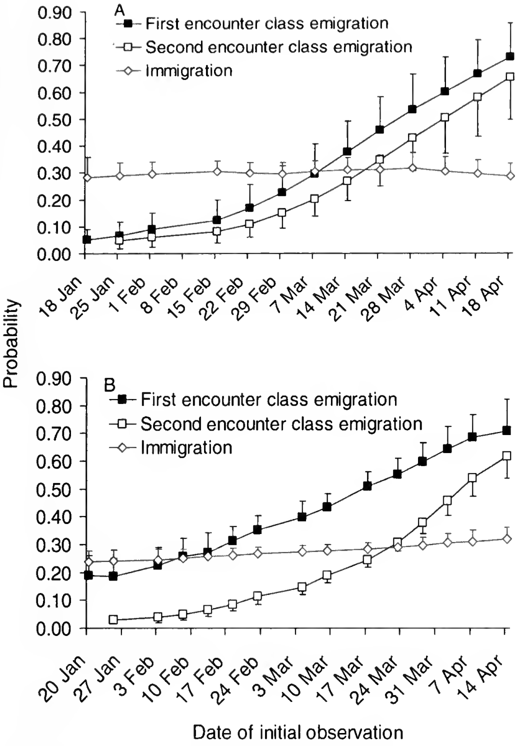

FIG. 2. Model average estimates (±1 SE) of immigration (◇) and emigration probabilities for first encounter class (■) and second encounter class (□) Black Brant during northward migration 2000 (A) and 2001 (B) in Humboldt Bay, California. First encounter class is a mixture of transients and residents; the second encounter class is entirely residents.

counter class structure) during model averaging. The model-averaged estimates (Fig. 2A) of emigration probabilities through time for birds observed in the first (mixture of transients and residents) and second (residents) encounter classes were similar in 2000.

The best immigration model for 2000 was $\{\gamma_c, p_T\}$, where seniority was constant and recapture probability followed a linear trend through time (Table 1). QAIC$_c$ weight was high for the best model. The only other model with appreciable weight had seniority following a linear trend through time, but this trend was not significantly different from constant (Fig. 2A).

Model Selection 2001.—The full model considered in 2001 $\{\phi_{e12 \cdot t}, p_t\}$ was an adequate general model to begin selection (deviance rank = 69/100). A variance inflation factor ($\hat{c}$ = 1.062) was applied to emigration and immigration model selection. The most parsimonious emigration model was $\{\phi_{e2 \cdot T}, p_t\}$ (Table 2). Residence had two encounter classes in this model that followed a linear trend through time. Recapture also varied through time. QAIC$_c$ weight was high for this model, and no others contributed much information to the model-averaged parameters (Fig. 2B).

The most parsimonious immigration model in 2001 was $\{\gamma_c, p_t\}$ (Table 2). Seniority was constant and recapture varied through time in this model. The next best immigration model had seniority following a positive linear trend through time (Fig. 2B).

Model Selection True Age.—We analyzed a subset of 171 birds observed 235 times in

TABLE 2. Model selection results (top 95% model set by weight) for Black Brant during January–May 2001 at Humboldt Bay, California, with $\hat{c}$ = 1.062 variance inflation factor, ϕ = residence probability, γ = seniority probability, and p = recapture probability. Model with zero ΔQAIC$_c$ is considered the most parsimonious. QAIC$_c$ weight is the relative strength of evidence supporting a given model.

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Parameters	QDeviance
Emigration					
$\{\phi_{e2*T}, p_t\}$[a]	1159.18	0.00	0.85	18	305.34
$\{\phi_{T^2}, p_t\}$	1163.87	4.68	0.08	16	314.15
$\{\phi_{e1t,e2T}, p_t\}$	1165.67	6.49	0.03	31	284.68
Immigration					
$\{\gamma_c, p_t\}$	1191.80	0.00	0.52	16	342.10
$\{\gamma_T, p_t\}$	1192.01	0.21	0.47	17	340.26
$\{\gamma_t, p_t\}$	1202.38	10.58	0.01	28	327.77

[a] Subscripts: t = time dependence (each week differs), c = constant through time, T = logit-linear trend through time, T^2 = quadratic trend through time, $e2$ = two encounter classes, $e1$ = transients and residents, and $e2$ = residents only.

TABLE 3. Model selection results for effects of true age as an individual covariate for Black Brant during January–May 2001 at Humboldt Bay, California, with $\hat{c}$ = 1.16 variance inflation factor, ϕ = residence probability, γ = seniority probability, and p = recapture probability. Model with zero $\Delta QAIC_c$ is considered the most parsimonious. $QAIC_c$ weight is the relative strength of evidence supporting a given model. Top 70% model set by weight for ϕ, and top 100% model set by weight for γ are shown.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Parameters	QDeviance
Emigration					
$\{\phi_{e2*T+age}, p_c\}$[a]	298.41	0.00	0.20	6	286.01
$\{\phi_{e2+T+age}, p_c\}$	298.92	0.51	0.15	5	288.64
$\{\phi_{e2*T*age}, p_c\}$	300.27	1.86	0.08	7	285.73
$\{\phi_{t+age}, p_c\}$	300.65	2.24	0.06	7	286.11
$\{\phi_{e2*T}, p_c\}$	300.79	2.38	0.06	5	290.50
$\{\phi_{e2+T}, p_c\}$	300.81	2.41	0.06	4	292.62
$\{\phi_{T+age}, p_c\}$	300.88	2.47	0.06	4	292.69
$\{\phi_{e2+t+age}, p_c\}$	302.44	4.04	0.03	8	285.75
$\{\phi_T, p_c\}$	302.53	4.12	0.03	3	296.42
Immigration					
$\{\gamma_t, p_c\}$	319.62	0.00	0.46	6	307.2
$\{\gamma_{t*age}, p_c\}$	320.26	0.64	0.34	11	297.1
$\{\gamma_{t+age}, p_c\}$	321.43	1.82	0.19	7	306.9
$\{\gamma_c, p_c\}$	326.24	6.63	0.02	2	322.2

[a] Subscripts: t = time dependence, c = constant through time, T = linear trend through time, and *age* = age individual covariate included.

2001 whose true ages were known for tests of true age effects on ϕ and γ. The general model tested for GOF was $\{\phi_{e6*t}, p_t\}$. This general model was sufficient (deviance rank = 76/100), but a variance inflation factor of $\hat{c}$ = 1.16 was applied. Model selection for ϕ indicated a transient effect, requiring two encounter classes. We detected a significant effect of true age on ϕ_t, but only weak evidence of a true age effect was detected for γ_i (Table 3). The relationship between age and ϕ was negative ($\beta = -0.456 \pm 0.231$, 95% confidence interval -0.908 to -0.004), indicating emigration probability was positively related with age. Thus, stopover duration was shorter for older birds than younger birds (Fig. 3). Temporal trends in emigration probability followed a pattern similar to that in the full data set (Fig. 2B). Chronology also differed by age, with older birds arriving at Humboldt Bay earlier than younger birds. In both 2000 and 2001, the median age of birds was highest in the first half of February (Fig. 4).

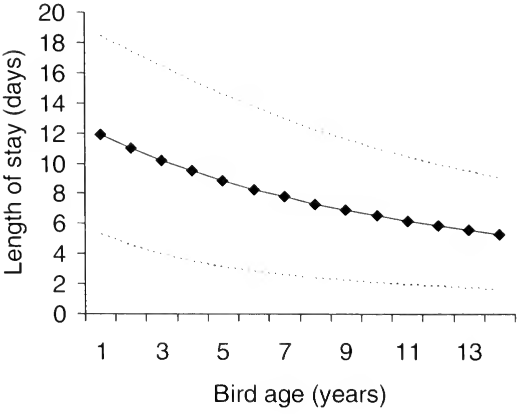

FIG. 3. Mean stopover duration in days as a function of true age for Black Brant at Humboldt Bay, California. Dashed lines indicate ±1 SE.

Techniques.—We detected 12 radio-marked Brant during January–May 2000. The first detection was on 20 February and the last radio-marked bird in the study area departed on 14 April. The GLM indicated that mean stopover duration measured by radiotelemetry (8 ± 3 days, range = 1–29 days, n = 12) was not significantly different from the CMR-derived estimate computed from residence probability alone (mean = 12 ± 2 days, z = 1.11, P = 0.268, n = 320). However, stopover duration measured by radiotelemetry was significantly different from the CMR-derived estimate computed from residence and immigration probabilities (mean = 21 ± 2 days, z = 2.83, P = 0.005, n = 320). This indicates the CMR-derived estimate computed from residence probability alone is preferred in this system.

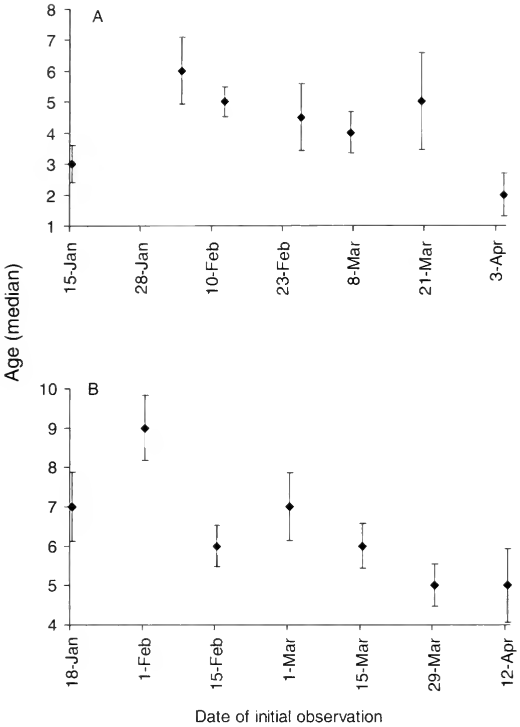

FIG. 4. Median true age (±1 SE) of newly observed Black Brant on Humboldt Bay by date during northward migration 2000 (A) and 2001 (B).

Stopover Duration.—Based on our comparison of techniques, we used the CMR-derived estimate computed from residence probability alone to compute stopover duration. Stopover durations were similar between years (Fig. 5), especially for birds in the second encounter class (residents). Residents that arrived ~25 January had stopover durations of ~36 days and stopover durations of both encounter classes decreased steadily throughout the season in both years (Fig. 5). Mean (±SE) stopover duration for all resident birds from 25 January to 11 April was 17 ± 2 days and for transient birds was 10 ± 1 days.

Volume.—The estimated total number of Brant using Humboldt Bay was 37,600 birds in 2000 and 77,800 birds in 2001. The total Pacific Flyway Brant population in 2000 was estimated at 135,000 birds, and we estimate that 28% and 58% of the population used Humboldt Bay in 2000 and 2001, respectively. Thirty-five percent of the population of radio-marked Brant (*n* = 34) used Humboldt Bay.

DISCUSSION

We found age-dependent variation in chronology and stopover duration. Our research indicated the older, more productive (Black and Owen 1995; Sedinger et al. 1998, 2001), and more dominant (Black et al. 1992) segment of the population made use of Humboldt Bay primarily early in the migratory season, and stayed for a shorter period than younger birds. Reproductive success in geese is dependent upon individuals getting to the farthest north stopover area early and maximizing time at that location (Palmer 1976, Madsen 2001). Thus, older birds were maximizing resource efficiency by spending less time at Humboldt Bay, a stopover site in the middle of the northward migration route, to arrive earlier at northern sites where reproductive success is determined (Madsen 2001).

Younger birds may take longer to gain condition for the next migratory flight due to lower foraging efficiency (Wunderle 1991), competitive exclusion by older, more dominant birds (Raveling 1970, Gauthreaux 1978, Black et al. 1992), or by encountering food resources depleted by earlier arriving older birds (Prop and Loonen 1989, Rowcliffe et al. 2004). Alternatively, a longer stopover could be a strategy to minimize energy reserve flux and increase survival of younger birds that are not likely to breed successfully in their early attempts. Life history theory predicts the tradeoff between somatic and reproductive investment would favor somatic investment in young ages of a "survivor" species (*sensu* Sæther et al. 1996) such as Brant to retain residual reproductive value (Stearns 1992).

Mean emigration probability in both years steadily increased with each time step from January to April, indicating a seasonally progressive migratory state. Thus, stopover durations were much shorter for birds arriving late in the migration versus those that arrived earlier (when true age is controlled), similar to other studies (Pradel et al. 1997b, Reed et al. 1998a, Prop et al. 2003). Humboldt Bay's "wintering" resident Brant population in January and early February was not entirely stable, with turnover from 3% to 8% per week until 15 February. This constant turnover in winter is evidence for steady, low-intensity movement of the Brant population, even dur-

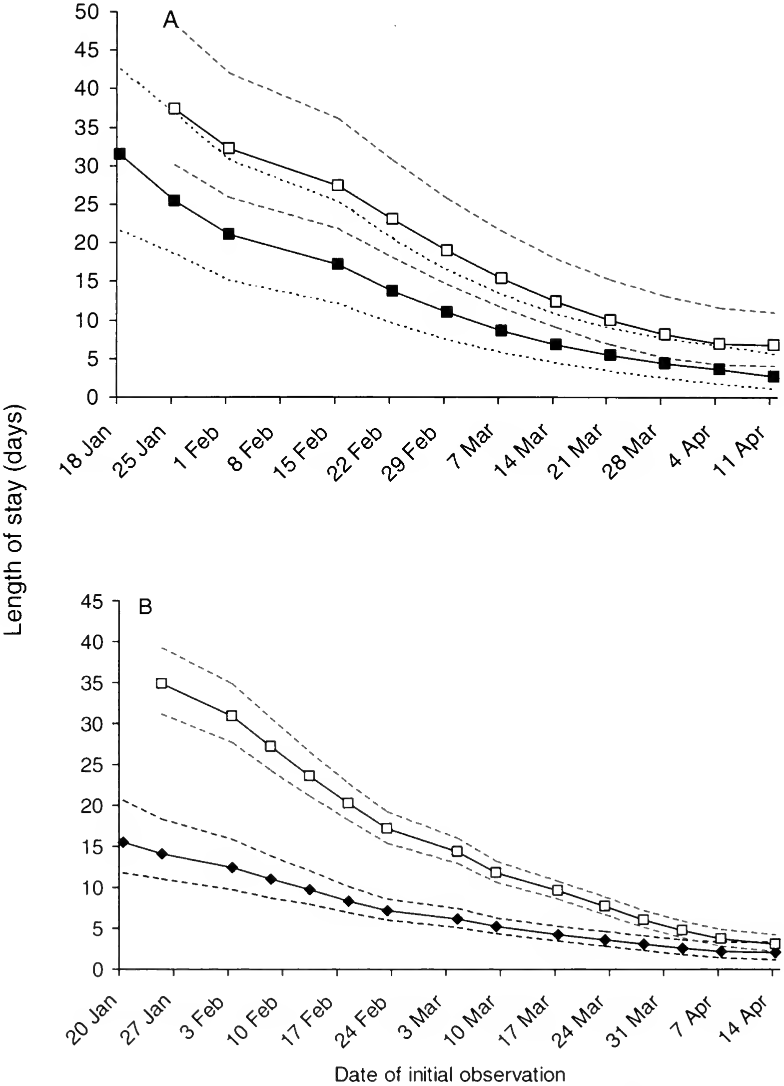

FIG. 5. Mean stopover duration in days (±1 SE) for first encounter class (■) and second encounter class (□) Black Brant at Humboldt Bay, California on a given date. Stopover duration for year 2000 (A), and 2001 (B). First encounter class is composed of a mixture of transients and residents; second encounter class is composed entirely of residents. Stopover durations were computed using model-averaged immigration and emigration parameters.

ing so-called winter residency. These findings agree with those of Reed et al. (1998a) who detected turnover rates of ~3% per week at Boundary Bay, British Columbia.

There was also variation in stopover duration due to individual heterogeneity. We detected a large proportion of transients in the population. Transients were birds with a zero residence probability after the initial encounter (*sensu* Pradel et al. 1997a). Transients were also detected in other studies of this population (Reed et al. 1998a, Routledge et al. 1999). Resident and transient status are problematic as there are no universally agreed upon definitions. Thompson (1993) defined a resident as a bird present in its final wintering area. However, considering migrations as a continuous and dynamic process involving multiple sites along the migratory route make defining a final wintering site problematic. We suggest a probabilistic framework for categorizing stopover sites by immigration and emigration probabilities, stopover durations, and volume. All birds are ultimately transient visitors to sites along migratory routes. Immigration and emigration probabilities and stopover duration provide universal metrics of that transience. Model selection procedures provide a framework for examining sources of variation in those metrics.

The distribution of minimum stopover durations (days between first and last observation) in our raw data approximated an inverse power curve. This is similar to the distribution reported by Routledge et al. (1999) for Brant staging at Parksville-Qualicum Beach, Vancouver Island, British Columbia. Our *a priori* model set did not include this inverse power curve distribution, but used encounter class structure (ϕ_{e2}) to control for the extreme heterogeneity between birds observed once, and those observed more than once. This structure allowed emigration estimates to differ for the encounter class composed of many transients versus the subsequent encounter class composed of residents. Transient models are useful tools to account for heterogeneity between groups of individuals. Transient models remove the substantial negative bias that transient animals can introduce to mean emigration estimates without sacrificing any data. Migrations are characterized by movements of large numbers of animals. Those that pause only briefly at a given stopover site should be included when considering use and impact of stopover habitats. More data and shorter time between observation periods might resolve the apparent curvilinear distribution of stopover durations, or the distribution may ultimately be most parsimoniously modeled by the encounter class structure used.

Routledge et al. (1999), incorporating the full distribution of stopover durations, estimated mean stopover duration for Brant in spring at Parksville-Qualicum Beach, British Columbia to be 5.92 days. This is significantly lower than our mean estimate from all birds for January to April at Humboldt Bay of 13 ± 2 days. However, Routledge et al.'s (1999) estimates came from a site much farther north, and used different methods. Reed et al.'s (1998a) estimates of mean stopover duration for spring at Boundary Bay, British Columbia, using methods similar to ours, were 8 days for transients and 27 days for residents. The differences between Reed et al.'s (1998a) and Routledge et al.'s (1999) results could be due to site-specific reasons. A comparison of methods at the same site would illuminate this disparity.

Our comparison of stopover duration estimators using radio-marked birds as a validation tool supported use of emigration alone to compute stopover duration (Reed et al. 1998a, Efford 2005), as opposed to using both immigration and emigration Schaub et al. (2001). Efford (2005) and the response by Pradel et al. (2005) indicate the Schaub et al. (2001) method performs well (is unbiased) when most birds spend the same amount of time at the stopover site, as is the case with many passerines (Bairlein 1986). However, in cases where stopover durations follow a Poisson distribution, the Schaub et al. (2001) method overestimates stopover duration by nearly double and the Reed et al. (1998a) method is preferred. Routledge et al. (1999) assumed that residence time distribution was an extended, negative binomial. Efford (2005) proposed another method that may be a good candidate for computing stopover duration. Another aspect of stopover duration deserving more attention is how the amount of time a bird has already spent at the stopover site affects its emigration probability (Pradel et al. 2005).

Conservation/management activity along flyways is usually based on peak counts achieved, and sites with the highest "internationally important" numbers receive priority in action plan prescriptions (e.g., Stroud 1992, Hunter and Black 1996, Black 1998). We could assume that at least 13% of the population made use of the site based on the average peak counts of Brant at Humboldt Bay (~17,000). Moore et al. (2004) ranked Humboldt Bay as the fourth most important site in the Pacific Flyway for Brant using this method. We calculated that 28% and 58% of the population used the Bay in the years 2000 and 2001, respectively using the more precise CMR estimates. Calculating the total volume of species that pass through migratory staging sites provides managers with more information with which to prioritize management action. In the last 100 years, California has lost more than 70% of its intertidal wetlands to anthropogenic alterations (Speth 1979). Eelgrass meadows of the Pacific Flyway on which Black Brant depend are particularly under threat from human activity (Ganter 2000, Moore et al. 2004, Ward et al. 2005). Migrants are often viewed as highly mobile, but the ability of individuals to find alternative sites when habitat is lost may not be assured (Dolman and Sutherland 1995, Ganter et al. 1997). Predicting the outcome of potential habitat change is a challenging procedure that relies on sound empirical data (Goss-Custard and Sutherland 1997, Pettifor et al. 2000). The large disparity between estimates of volume for the two years of this study indicate the need for repeated sampling efforts to increase precision and elucidate sources of annual variation.

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PARENTAL INVESTMENT IN SWAN GEESE IN AN URBAN ENVIRONMENT

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ABSTRACT.—I studied brood-rearing behavior of introduced Swan Geese (*Anser cygnoides*) in Heidelberg, Germany during 2002 and 2003. Two hypotheses were tested: (1) division of labor between males and females is similar to that of wild *Anser* species, and (2) parental investment (vigilance behavior) is adjusted for brood size. I used 10-min sessions of focal animal sampling during which I simultaneously recorded the behavior of the male, the female, and a majority of the juveniles every 15 sec. Division of labor was similar to that observed in wild *Anser* populations: males were more vigilant whereas females spent more time feeding during the first 4 weeks of brood-rearing. As brood-rearing progressed, vigilance and agonistic behavior by both males and females decreased, whereas juveniles decreased feeding and increased vigilance. Adults (males and females combined) adjusted vigilance for brood size. A general linear model showed a significant influence of both brood size and brood age on parental vigilance. *Received 12 February 2004. Accepted 12 July 2006.*

During brood rearing, females of most species of wild *Anser* geese usually spend more time feeding than males to compensate for energy loss during incubation. Males spend more time being vigilant, i.e., looking for predators (Afton and Paulus 1992). This division of labor by gender was found in time budget studies of many goose species (Afton and Paulus 1992).

Concerning brood size, larger groups of goslings should receive more vigilance by their parents than smaller groups as parental investment is considered to be "shared" (Lessells 1987). This hypothesis suggests that parental care might be adjusted for brood size by devoting more time to vigilance as brood size increases ("shared" parental investment). The "unshared" parental investment hypothesis suggests that parental vigilance should not be adjusted for brood size, since any time devoted to vigilance benefits all goslings simultaneously, regardless of brood size. Some empirical tests found an adjustment of parental investment (e.g., the level of vigilance) to brood size (Sedinger and Raveling 1990, Forslund 1993, Siriwardena and Black 1999) and others did not (Lazarus and Inglis 1978, Lessells 1987, Schmutz and Laing 2002). However, gosling age is another important variable since mortality of goslings is highest during the first 2–3 weeks of life (Owen 1980, Forslund 1993).

Behavior of introduced geese has rarely been studied (e.g., Randler 2003a, 2003b), and little is known about their brooding behavior. Studies of introduced geese in an urban environment, where most natural predators are absent, may clarify the complimentary hypotheses of parental care in geese. Furthermore, parental investment in neither wild nor introduced Swan Geese (*Anser cygnoides*) has been examined. Since this species is critically endangered (Goroshko 2001), studies of introduced populations may be of conservation interest. The objectives of this study were to examine (1) whether parental care (time budgets and division of labor between males and females) of introduced Swan Geese is similar to that of wild populations, and (2) the relationship between brood size (number of goslings) and parental care (as measured by vigilance).

METHODS

The Swan Goose is a non-native species in Europe, having been introduced in the 18th century (Delacour 1954). The study flock in Heidelberg, southwestern Germany (8° 41′ E, 49° 25′ N) was established in the 1990s. The birds breed on an island in the Neckar River and soon after hatching, families move to feed on a lawn which extends 1.1 km along the river. In 2002 and 2003, I studied 13 families of Swan Geese (140 individuals in 2002 and 174 in 2003) during brood rearing (Randler 2003a, 2003b).

I used instantaneous focal animal sampling (Altmann 1974) to detect differences between males and females, and identify rare behaviors

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that may be overlooked during flock scans (Baldassarre et al. 1988). Sampling sessions were 10-min/family, during which I recorded the behavior of the male, female, and a majority of the juveniles. Goslings could not be identified individually and I recorded the behavior displayed by the majority of the brood at each instantaneous sample (Schmutz and Laing 2002). The order of sampling families was random. I used 15-sec sampling intervals because this interval provides data that are close to continuous observations (Pöysä 1991). I recorded the following behavioral categories (adapted from McWilliams and Raveling 1998): feeding, resting, walking, comfort behavior (preen, stretch, shake, or scratch), vigilance (neck stretched upward to full length), and agonistic interaction (intraspecific aggressive encounters). Sampling was conducted between 0900 and 1600 hrs (Central European Summer Time) and only when families were on land. If disturbed during sampling (e.g., by dogs; Randler 2003a), families escaped into the water and sampling continued (if necessary) after the geese returned to land. Some bias may be present because data collection was only done during certain daytime periods. This seems unlikely, because time of day does not strongly influence behavior of families with goslings (Lazarus and Inglis 1978, Forslund 1993, Schmutz and Laing 2002).

I separated samplings into 4-week periods of brood rearing (weeks 1–4, 5–8, and 9–12), because parental investment may differ between these periods (Forslund 1993) and goslings were more prone to predation during their first weeks of life (Owen 1980). I chose these sampling periods because at 8 weeks, most juveniles were close to fledging (i.e., capable of sustained flight; Kolbe 1999). Family bonds extend over the brood rearing period and sampling during week 9–12 allows comparison of the brood rearing period with the post-fledging period.

Some studies report between-year differences in time budgets (Schmutz and Laing 2002). Because vigilance did not differ between years I pooled years. An unknown number of individuals may have been sampled in both years and my data may include replicated observations of the same birds. In addition to the 6 (2002) and 7 (2003) families studied, I also sampled 17 non-breeders of unknown gender between 31 May and 26 June 2002 using the same focal-animal sampling method.

Gender of adults was assigned by knob size, bill size, body size, and behavior. Females had shorter and thinner bills, and shorter necks (Madge and Burn 1988, Ogilvie and Young 1998); males swam behind broods (Bauer and Glutz von Blotzheim 1968, Rutschke 1997). Family sample sizes by periods were 13 (weeks 1–4), 8 (weeks 5–8), and 9 (weeks 9–12); I sampled each family between one and five times during each period. I first calculated the mean for each family (male, female, juveniles) by sampling period and then calculated the means of the three sampling periods. Parental vigilance is the mean of male and female vigilance. Some post-hatching brood amalgamation took place, at times forming families including 3 adults. One "family" of 13 juveniles was led by 4 adults. I did not use amalgamated families in the analyses.

I expressed behaviors (e.g., feeding, vigilance, etc.) as percentages of total time budget (square-root arcsine transformed). To compare percentages between different groups, I used the Mann-Whitney U test on untransformed data and, to compare dependent variables, I used Wilcoxon matched-pairs signed rank test. I used Pearson's correlation to examine the relationship between vigilance and brood size ($\log_{10}$ transformed). I used a general linear model (GLM) with year and period as fixed factors, number of juveniles ($\log_{10}$) as a covariate and parental care (vigilance) as the dependent variable. I used R^2 as a measure of explained variance. I used SPSS version 11.0 to analyze the data (Bühl and Zöfel 2002) and set statistical significance at $P < 0.05$.

RESULTS

The first goslings appeared on the feeding grounds during the last 10 days of May. Brood sizes did not remain stable during the study period because of predation. I observed two unsuccessful predation attempts, one by Carrion Crows (*Corvus c. corone*) and one by Yellow-legged Mediterranean Gulls (*Larus michahellis*), both of which bred nearby. Brood sizes were 4.3 ± 1.4 ($\bar{x}$ ± SE) in 2002 and 3.5 ± 0.7 in 2003 during week 1–4.

TABLE 1. Time budgets (%, means ± SE) of male, female, and juvenile Swan Geese during three different periods of brood rearing in 2002 and 2003 in Heidelberg, Germany. Each family was sampled between one and five times during each period. The mean of each family per period was used to calculate percentages to not over-represent some families. Differences between either males or females and goslings are expressed as $^{*}P < 0.05$; $^{**}P < 0.01$.

	Feeding	Resting	Walking	Comfort	Vigilant	Agonistic
FAMILIES	Weeks 1–4					
n = 13						
Male	27.7 ± 3.0^{b**}	3.2 ± 1.6	2.5 ± 0.8	10.6 ± 4.0	51.1 ± 4.1^{a**}	4.2 ± 1.0
Female	41.4 ± 4.7^{b**}	4.8 ± 2.0	2.2 ± 0.7	7.0 ± 2.1	39.9 ± 4.9^{a**}	3.8 ± 1.1
Juvenile	75.5 ± 5.0	11.2 ± 3.9	5.7 ± 1.8	5.9 ± 1.9	0.6 ± 0.2	0.0 ± 0
Parental	34.6 ± 3.4	4.0 ± 1.5	2.4 ± 0.7	8.8 ± 2.7	45.5 ± 3.7	4.0 ± 0.9
FAMILIES	Weeks 5–8					
n = 8						
Male	35.1 ± 8.7^{b*}	7.6 ± 3.4	4.4 ± 1.5	15.4 ± 4.5	34.5 ± 5.9^{a*}	1.5 ± 0.7
Female	29.4 ± 7.3^{b*}	9.6 ± 3.0	4.4 ± 1.5	23.6 ± 5.0	29.5 ± 4.1^{a*}	1.7 ± 0.7
Juvenile	62.8 ± 12.0	10.1 ± 3.8	2.6 ± 1.1	18.8 ± 8.7	4.1 ± 0.8	0.0 ± 0
Parental	32.2 ± 7.5	8.6 ± 3.0	4.4 ± 1.5	19.5 ± 4.7	32.0 ± 3.8	1.6 ± 0.7
FAMILIES	Weeks 9–12					
n = 9						
Male	31.8 ± 6.9^{b**}	14.7 ± 6.5	3.4 ± 1.3	17.2 ± 5.2	29.8 ± 4.0^{a**}	1.5 ± 0.7
Female	37.4 ± 5.7^{b**}	15.3 ± 5.7	3.8 ± 1.4	13.7 ± 5.0	24.4 ± 2.6^{a**}	3.2 ± 1.3
Juvenile	57.1 ± 9.2	23.1 ± 8.8	3.6 ± 1.0	12.2 ± 5.8	2.8 ± 1.1	0.1 ± 0.1
Parental	34.6 ± 5.3	15.0 ± 6.0	3.6 ± 1.3	15.4 ± 4.4	27.1 ± 2.6	2.3 ± 0.7
FAMILIES	Weeks 1–12					
n = 30						
Male	30.9 ± 3.3	7.8 ± 2.3	3.3 ± 0.6	13.9 ± 2.6	40.3 ± 3.1	2.7 ± 0.6
Female	37.7 ± 3.3	9.3 ± 2.1	3.3 ± 0.6	13.4 ± 2.4	32.2 ± 2.7	3.0 ± 0.6
Juvenile	66.6 ± 4.8	14.5 ± 3.3	4.3 ± 0.9	11.2 ± 3.0	2.2 ± 0.4	0.0 ± 0.0
Parental	34.0 ± 2.8	8.5 ± 2.1	3.3 ± 0.6	13.6 ± 2.2	36.4 ± 2.2	2.8 ± 0.5
Non-breeders	39.1 ± 6.1	22.1 ± 6.8	11.3 ± 2.2	14.4 ± 4.1	12.8 ± 2.3	0.0 ± 0.0
n = 17						

[a] Value higher than goslings. Non-breeders depicted for comparison.
[b] Value lower than goslings. Non-breeders depicted for comparison.

Means per period (both years pooled) were 3.9 ± 0.7 (week 1–4), 3.6 ± 1.1 (week 5–8), and 3.6 ± 1.0 (week 9–12).

Time Budgets.—Non-breeding adults spent less time vigilant (Table 1) compared with male (Mann-Whitney U test: $Z = -4.584$, $P < 0.001$, $n = 30$), female ($Z = -3.998$, $P < 0.001$, $n = 30$), and parental vigilance (mean of male and female in each pair: $Z = -4.416$, $P < 0.001$, $n = 30$; based on the overall means from weeks 1–12). Within families, females, spent more time feeding (Wilcoxon test $Z = -2.750$, $P = 0.006$, $n = 13$) during weeks 1–4 but not in weeks 5–8 and 9–12 ($P > 0.05$) and, a lower proportion of time vigilant than males during weeks 1–4 ($Z = -2.202$, $P = 0.028$, $n = 13$), but not during periods 2 and 3 (Wilcoxon-test, $P > 0.05$; Table 1).

Goslings fed more than both their parents and their vigilance was lower (Table 1). During brood rearing, males reduced their vigilance between periods 1 and 3 (Wilcoxon test: $Z = -2.201$, $P = 0.028$, $n = 7$), and their agonistic behavior between periods 1 and 2 ($Z = -1.997$, $P = 0.046$, $n = 6$). Other behaviors did not change ($P > 0.05$). Females reduced agonistic behavior between periods 1 and 2 ($Z = -1.892$, $P = 0.05$, $n = 6$) and vigilance between periods 1 and 3 ($Z = -2.197$, $P = 0.028$, $n = 7$).

Parental Care.—Mean parental care (vigilance) per period varied (Table 1). There was correlational evidence for an adjustment of parental vigilance to brood size for periods 1 and 3 (period 1: $r = 0.557$, $P = 0.048$, $n = 13$; period 2: $r = 0.617$, $P = 0.10$, $n = 8$; period 3: $r = 0.753$, $P = 0.019$, $n = 9$). Vigilance was dependent on brood size and period but not year (Total model: $F_{6,23} = 7.847$, $P < 0.001$; brood size $F_1 = 16.599$, $P < 0.001$;

period: $F_2 = 10.051$, $P = 0.001$; year: $F_1 = 2.446$, $P = 0.13$; all interaction terms: $P > 0.10$). Adults of larger broods were more vigilant and vigilance declined through the stages of brood rearing. The total amount of explained variance was high ($R^2 = 0.672$, corrected $R^2 = 0.586$).

DISCUSSION

Time Budgets.—Non-breeders were less vigilant, similar to the findings of others (Lessells 1987, Forslund 1993). Adult geese of different species with broods usually spend between 15 and 45% of their time feeding and 40–45% vigilant to look for predators to protect and warn their goslings (Afton and Paulus 1992). Other studies also found marked differences among adult males, females, and juveniles within broods (Austin 1990, Schmutz and Laing 2002). Females spend more time feeding than males (Lazarus and Inglis 1978, Lessells 1987, Sedinger and Raveling 1990). Males, in turn, spend more time vigilant, similar to the results of the present study. Juveniles fed during a large part of their time similar to other goose species (Afton and Paulus 1992), because juveniles have higher nutritional demands. Afton and Paulus (1992) also present examples for decreasing vigilance during maturation of broods (also Lazarus and Inglis 1978). I also found a decrease in vigilance in Swan Geese. Thus, my study shows that introduced geese have similar behavioral patterns during brood rearing as wild geese.

Parental Care.—Parental vigilance during the brood rearing period was related to brood size and this relationship extended into the post-fledging period. These results support the "shared" parental investment hypothesis. Differences among studies about parental investment and brood size may be caused by brood size as my study covered a wide range of family sizes from 1 to 10 goslings. Age of goslings may have an important role in affecting vigilance behavior (Forslund 1993).

The major conclusion of the study is that introduced Swan Geese have similar parental care and division of labor between gender compared to wild Swan Geese, and to other *Anser* species.

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USE OF NEST BOXES BY GOLDENEYES IN EASTERN NORTH AMERICA

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ABSTRACT.—We evaluated and monitored use of 105–133 nest boxes by Common Goldeneye (*Bucephala clangula*) and Barrow's Goldeneye (*Bucephala islandica*) during 1999–2004 on 60 lakes of high plateaus of the Laurentian Highlands, in the boreal forest of Québec, Canada. Only three species of birds used nest boxes regularly, American Kestrel (*Falco sparverius*), Barrow's Goldeneye, and Common Goldeneye. The proportion of nest boxes used by goldeneyes in 2000–2004 ranged from 23 to 43% whereas hatching success ranged from 37 to 67%. Successful Barrow's and Common goldeneye clutches averaged 6.76 ± 0.38 (SE, n = 29) and 7.77 ± 0.44 eggs (n = 31), respectively. Predation in nest boxes was not a major mortality factor. Goldeneyes used all nest boxes independent of their location but reproductive success was lower in nest boxes 25–160 m from shore in clearcuts. The number of Barrow's and Common goldeneye breeding pairs increased between 1999 and 2003, but number of broods remained stable after an increase in 2000. *Received 15 December 2005. Accepted 12 August 2006.*

The eastern population of Barrow's Goldeneye (*Bucephala islandica*) is estimated at ~1,400 pairs (Robert et al. 2000a) and was classified as Special Concern by the Committee on the Status of Endangered Wildlife in Canada in November 2000 (COSEWIC 2006). Its breeding range has been discovered only recently in the Québec Laurentian Highlands, on the north shore of the St. Lawrence River estuary and gulf (Robert et al. 2000b). It breeds on small lakes, often without fish at >500 m in elevation (Robert et al. 2000b), where tree growth is slow and large trees with suitable nest cavities are apparently rare (MR, pers. obs.). Forests in its breeding area are under intense logging pressures (Robert et al. 2000a) and availability of suitable nesting cavities is an issue of concern.

Nest boxes have been used successfully to locally increase the abundance of cavity-nesting waterfowl (McLaughlin and Grice 1952, Johnson 1967, Nichols and Johnson 1990) and to establish new populations (Doty and Kruse 1972, Eriksson 1982, Dennis and Dow 1984). Barrow's Goldeneyes have readily used nest boxes in British Columbia (Savard 1985, 1988) and their use has increased the number of broods locally. The small Icelandic population uses nest boxes as well (JPS and MR, pers. obs.). Nest boxes have been useful in reducing the impact of logging on Common Goldeneyes (*Bucephala clangula*) in Scandinavia (Cramp and Simmons 1977). Nest-box programs have proven successful overall for most cavity-nesting ducks (Zicus 1990, Hepp and Bellrose 1995, Eadie et al. 1995), but potential problems could reduce their efficiency. These include increased predation rates, nest parasitism, and increased competition for adequate brood-rearing ponds (Andersson and Eriksson 1982, Savard 1988, Eadie et al. 1995, Evans et al. 2002, Pöysä and Pöysä 2002). Nest boxes in British Columbia had larger clutch sizes, lower nesting success, and a different suite of predators than natural nests (Evans et al. 2002). There is also the underlying risk that nest-boxes may attract predators and become ecological traps (Battin 2004). A related concern is inter-specific competition between Barrow's and Common goldeneyes, which use similar nest sites and exclude each other from pair and brood territories (Savard 1982, 1984), and are known to occasionally hybridize (Martin and Di Labio 1994).

We examined use of nest boxes by Barrow's Goldeneyes in their high elevation breeding habitat. Specifically we: 1) evaluated use of nest boxes by goldeneyes and other wildlife in the only known Barrow's Goldeneye habitat accessible by road, 2) measured goldeneye reproductive success in nest boxes, 3) compared nest-box use in relation to box location, and 4) compared the relative abundance of Common and Barrow's goldeneye pairs and broods.

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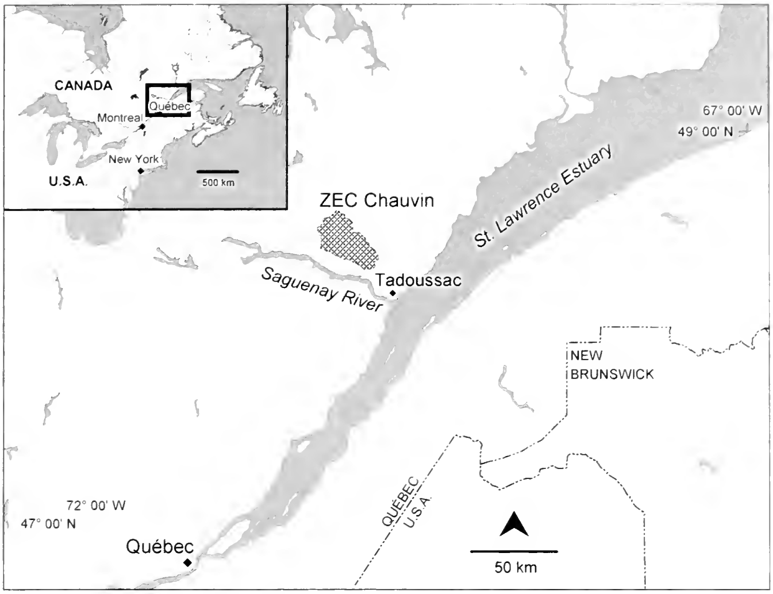

FIG. 1. Goldeneye nest box study area (ZEC Chauvin) in the Laurentian Highlands north of the St. Lawrence River estuary, in the boreal forest of Québec, Canada.

METHODS

Study Area.—The study was conducted in the Zone d'exploitation controlée (ZEC) Chauvin, a 610-km^2 area ~40 km northeast of Tadoussac (48° 09′ N, 69° 43′ W), Québec, Canada (Fig. 1). ZEC Chauvin is on high plateaus of the Laurentian Highlands, north of the St. Lawrence River estuary, in the balsam fir (*Abies balsamea*)-white birch (*Betula papyrifera*) bioclimatic domain of the boreal forest. Mean annual temperature and precipitation are 0.0° C and 1,300 mm (35% as snow), respectively (Robitaille and Saucier 1998). Common and Barrow's goldeneye pairs and broods use the lakes of this area (Robert et al. 2000a), which is under intense forest exploitation and is managed for hunting, fishing, and other recreational activities.

Nest Boxes.—We installed 111 nest boxes in August–September 1998 at 37 lakes in the study area, three per lake: one above water on a steel post (mean distance from shore = 6.6 m, range = 3–18; mean height above water = 1.4 m, range = 0.08–2.2), one on a tree at the edge of the lake (mean distance from water edge = 4.1 m, range = 0.8–12.7; mean height above ground = 4.0 m, range = 3.4–4.5), and one on a tree or snag in a recent clearcut (mean distance from water edge = 74.6 m, range = 25–160; mean height above ground = 4.0 m, range = 3.3–5.3). We also installed 25 single nest boxes in September 1999 on a tree or snag in clearcuts near additional lakes. All nest boxes were highly visible, measured 24 × 22 × 60 cm, and had an entrance hole measuring 10 × 13 cm. Nest boxes were checked between 1999 and 2004, at least twice in 1999 (once in mid incubation and once after hatching) and usually at least three times in 2000–2004, with a first visit at the end of egg-laying. Occupied boxes were checked more often (i.e., 4–6 times) to better estimate clutch size and capture females. Sixteen Barrow's Goldeneye females were captured in nest boxes and fitted with backpack radio-transmitters in 2001–2003 to study brood ecology. None was recaptured or seen again on the study area in 2002–2004 (Robert et al. 2006).

Pair and Brood Counts.—We conducted Barrow's and Common goldeneye pair and brood surveys in a 217-km^2 area of ZEC Chauvin encompassing all lakes with three nest boxes, as well as 19 of 25 lakes with single boxes. This area includes 239 lakes (mean = 5.4 ha, SD = 11.3, range = 0.01–115), of which 132 are <2 ha. We surveyed goldeneye pairs on 60 lakes of this area each

TABLE 1. Number of goldeneye nest boxes used[a]; boxes were installed in fall 1998 (n = 111) and 1999 (n = 25) in the boreal forest of Québec, Canada.

	1999	2000	2001	2002	2003	2004
Barrow's/Common goldeneyes	1	30	35	56	54	36
American Kestrel[b]	12	22 (1)[c]	27 (1)[c]	27 (3)[c]	8 (1)[c]	2
Hooded Merganser[b]	0	0	0	2 (3)[c]	0 (3)[c]	2
Tree Swallow (*Tachycineta bicolor*)	3	2	0	0	0	0
Northern Flicker (*Colaptes auratus*)	1	1	1	0	1	0
Red Squirrel[b]	0	1	8 (1)[c]	4	8 (7)[c]	3 (1)[c]
Boxes available	105	133	127	130	133	128
Boxes used	17	56	71	89	71	43
Percent used	16	42	56	69	53	34

[a] At least one egg was found or in the case of squirrels, a nest.
[b] Some nest boxes were used by more than one species during a given year.
[c] The number in parenthesis represents species in double occupancy.

year between 21 May and 28 June 1999–2003. We surveyed most (75%) lakes only once in 1999 (late May), and most (>75%) at least twice in subsequent years (late May and in early to mid-Jun). All goldeneyes were recorded as pair, lone adult male, lone adult female, groups of adult males and/or females, and immature female or male (i.e., second-year [SY] individuals). We used the maximum number of adult males seen on each particular lake in a given year summed across all lakes to derive a measure of pair abundance in the study area. We also surveyed goldeneye broods on the same lakes. Survey efforts were less intensive in 1999 when 27% of the lakes were surveyed once and 46% twice during the brood season (20 Jun to 11 Sep). From 2000 to 2003, most lakes (77%) were surveyed ≥3 times. We used head shape and color, bill shape, and wing pattern to separate Common and Barrow's goldeneye females (Tobish 1986). Adult and immature females were separated by iris color (Tobish 1986). We combined the number of immature females identified with the number of females of undetermined age (there were few and most were likely immatures), as an estimate of immature abundance in the study area.

Statistics.—Means ± SE are presented. We used analysis of variance to compare means. Differences in frequency were tested using χ^2 and Pearson's standardized residuals (Agresti 2002). All nest boxes were used to estimate the overall use of nest boxes by wildlife, but analysis of nest-box use in relation to location was limited to lakes with properly located trios of boxes (n = 29–35 lakes).

RESULTS

Nest Boxes.—Between 105 and 133 boxes were available yearly (1999–2004), and were used by six species of birds (Table 1). The proportion of boxes used increased from 16% in 1999 to 69% in 2002, and decreased to 34% in 2004. Barrow's and Common goldeneyes were the major users in all years but 1999 followed by American Kestrels (*Falco sparverius*). Kestrels dominated box use in 1999 (n = 12) and their use peaked in 2001 (n = 27) and 2002 (n = 27) before abruptly decreasing in 2003 (n = 8) and 2004 (n = 2). Hooded Mergansers (*Lophodytes cucullatus*) used boxes in 2002 and 2004 (two nests each year). Some boxes were used by more than one species in the same year. Six cases each involved goldeneyes and American Kestrels, and goldeneyes and Hooded Mergansers. Eight involved goldeneyes nesting on unoccupied red squirrel (*Tamiasciurus hudsonicus*) nests, of which seven successfully hatched. There was one instance of an American Kestrel nesting on a red squirrel nest.

Both Common and Barrow's goldeneyes used nest boxes (Table 2), although the relative use by each species could not be ascertained because of the large proportion of boxes where species of goldeneye could not be identified. Only one box was used by goldeneyes in 1999. Box use increased to 30 in 2000, peaked at 56 and 54 in 2002 and 2003 respectively, and decreased to 36 in 2004. Goldeneye hatching success (≥1 egg hatching) ranged between 37 and 67% (Table 3). Eighty-five of 110 nest failures (no egg hatch-

TABLE 2. Number of nest boxes used by Barrow's and Common goldeneyes; boxes were installed in fall 1998 (n = 111) and 1999 (n = 25) in the boreal forest of Québec, Canada.

	1999	2000	2001	2002	2003	2004	Totals[a]
Number of boxes	105	133	127	130	133	128	651
Barrow's Goldeneye	0	9	7	12	11	4	43
Common Goldeneye	0	9	10	19	9	6	53
Goldeneye sp.	1	12	18	25	34	26	115
All goldeneyes	1	30	35	56	54	36	212
Used by goldeneyes (%)	1	23	28	43	41	28	33

[a] Excludes 1999.

ing) were associated with partial or complete egg loss, 15 with no egg loss, and 10 for which egg loss could not be ascertained. Only 28 nests had obvious signs of predation (i.e., broken eggshells or presence of dry yolk) and at least 10 females successfully hatched eggs in spite of partial egg loss (1–5) during incubation. There were no signs of predation or broken eggs in all cases. More nest failures occurred after incubation had started (57%, n = 107 nests).

Four clutches had >12 eggs (13–15). All boxes with <3 eggs were unsuccessful, but five of eight 3-egg clutches and two of six 4-egg clutches were successful. A similar proportion of <6-egg (32.7%, n = 49) and >9-egg (36.4%, n = 22) clutches hatched successfully (χ^2 = 0.093, P = 0.76, df = 1). Clutches of 6–9 eggs had a greater (67.1%, n = 70) hatching success than clutches with <6 eggs (χ^2 = 13.7, P < 0.001, df = 1) and >9 eggs (χ^2 = 6.6, P = 0.01, df = 1). The average clutch size of successful goldeneyes increased during the first 3 years (2000 = 7.22 ± 0.55 eggs, n = 18; 2001 = 7.85 ± 0.37, n = 13; 2002 = 8.13 ± 0.68, n = 15) and decreased in the next 2 years (2003 = 7.31 ± 0.71, n = 16; 2004 = 6.78 ± 0.92, n = 9). These changes are not significant (F = 1.23, P = 0.30). Successful Barrow's Goldeneye clutches were smaller (6.76 ± 0.38, n = 29) than those of Common Goldeneyes (7.77 ± 0.44, n = 31; F = 3.0, P = 0.088). The same difference was observed for unsuccessful clutches (6.62 ± 0.36, n = 37 vs. 7.52 ± 0.35, n = 46; F = 3.17, P = 0.079).

TABLE 3. Nest success of goldeneyes in nest boxes installed in fall 1998 (n = 111) and 1999 (n = 25) in the boreal forest of Québec, Canada.

		Nest fate		
Year	Nests	Hatched[a] (%)	Failed (%)	Unknown (%)
1999	1	0	100	0
2000	30	67	27	7
2001	35	40	57	<1
2002	56	37	61	<1
2003	54	41	56	<1
2004	36	53	47	0
Totals	212	45	52	<1

[a] At least one egg hatching.

Goldeneyes used all boxes independently of their location (above water, along shoreline or >25 m from shore) in all years (Table 4; χ^2 = 5.50, P = 0.70, df = 8). Goldeneyes using nest boxes in clearcuts were slightly less successful (40%, n = 86) than those using boxes along the shoreline (56%, n = 63) or above water (50%; n = 56, χ^2 = 4.51, P = 0.11, df = 2). Pearson's standardized residuals confirmed that boxes in clearcuts were less successful than others (above water = 0.45; along shoreline = 1.71; in clearcuts = −2.00). American Kestrels clearly preferred nest boxes away from water, having used 54 boxes/191 (28%) in clearcuts versus only 10/382 (3%) at the other two locations (χ^2 = 63.3, P < 0.001, df = 1).

Pair and Brood Counts.—There were nearly three times more Barrow's than Common goldeneye males on the study area in 1999 (Table 5). Barrow's and Common goldeneyes had increased from 28 to 43 and from 10 to 46 estimated pairs, respectively, in 2003. The number of immature (SY) females varied between years. The contrast in numbers for both species combined was especially great between 2000 (n = 9) and 2001 (n = 74). This greater number of immatures in 2001 was followed by a marked increase in the number of pairs of both species in 2002. A peak in the

TABLE 4. Location of nest boxes used by goldeneyes; nest boxes were installed in fall 1998 (n = 111) and 1999 (n = 25) in the boreal forest of Québec, Canada.

Year	Nests (Lakes)[a]	N occupied	Occupied (%)		
			Above water	Shoreline	In clearcut
1999	93 (31)	1	1	0	0
2000	102 (34)	30	27	47	27
2001	87 (29)	27	33	33	33
2002	93 (31)	43	37	37	26
2003	105 (35)	44	27	36	36
2004	93 (31)	20	45	20	35

[a] Three nest boxes per lake (one above water, one along the shoreline, and one >25 m from shore).

number of immatures occurred in 2002, followed by an increase in the number of Common Goldeneye pairs in 2003. This increase in pairs did not yield a proportional increase in the number of broods of either species. The brood/pair ratio doubled between 1999 and 2000 and decreased in following years (Table 5).

DISCUSSION

This study is the first to examine use of nest boxes by Barrow's Goldeneye in eastern North America. Goldeneyes were the main users of nest boxes in the study area, confirming their usefulness as a potential management tool in the boreal forest of the Laurentian Highlands. The only other important user of nest boxes in the study area was the American Kestrel. Nest boxes allowed this species to exploit temporary new open habitats created by logging, whereas vegetation regrowth may have contributed to their low use in 2003 and 2004. Rohrbaugh and Yahner (1997) found that boxes frequently used by American Kestrels were associated with extremely open habitat dominated by herbaceous vegetation. The preference of kestrels for nest boxes in clearcuts may be related to the more centralized position of these boxes within the territory which likely allows adults to better protect the nest.

The large increase in nest box use in 2002 corresponds to the time females hatched in 2000 would have initiated first breeding. The decrease in 2003 and especially 2004 may be due to the suspected over winter mortality of several successfully reproducing adult Barrow's Goldeneye females (Robert et al. 2006). Goldeneye hatching success was similar to that reported elsewhere (Savard 1988, Evans et al. 2002). Nest desertion was the major cause of failure similar to other studies (Grenquist 1963, Rajala and Ormio 1970, Eadie et al. 2000). We suspect that competition for nest sites (Erskine 1960, 1990; Lumsden and Wenting 1976), a large number of first year breeders (Grenquist 1963), and disturbances related to fishing may have contributed to the high level of nest desertion. Eadie et al. (1995, 2000) indicated that true clutch size of a single female goldeneye is probably 6–9 eggs. Hatching success of clutches in that range was

TABLE 5. Abundance of Common and Barrow's goldeneyes on 60 lakes of ZEC Chauvin, in the boreal forest of Québec, Canada.

Year	Barrow's Goldeneye				Common Goldeneye			
	Pairs[a]	Broods	Brood/pair	SYF	Pairs[a]	Broods	Brood/pair	SYF
1999[b]	28	10	0.36	12	10	4	0.40	1
2000	24	17	0.71	6	13	11	0.85	3
2001	33	17	0.52	49	13	9	0.69	25
2002	42	15	0.36	70	28	11	0.39	67
2003	43	14	0.33	44	46	7	0.15	49

[a] Pairs + unpaired males.

[b] Number of SY females unreliable for 1999 because only one survey (late May–early Jun) of most (75%) lakes; the number of broods is likely underestimated in 1999.

higher in our study than in smaller and larger clutches. Large clutches are likely caused by nest parasitism, which is frequent in goldeneyes, and often results in nest desertion (Eriksson and Anderson 1982, Eadie and Fryxell 1992). Smaller clutches are often the result of first year breeders which are more prone to desertion (Eadie et al. 2000). Our smallest incubated clutch was three eggs ($n = 8$, 5 hatching); the previously reported smallest one was four eggs (Eadie et al. 1995, 2000).

Goldeneyes used nest boxes independently of their location. The tendency of fewer goldeneyes using clearcut boxes from 2000 to 2002 may be related to the preference of kestrels for boxes in clearcuts. Goldeneyes used nest boxes at all three locations similarly in 2003–2004 when kestrel use of boxes was low. Pöysä et al. (1999) reported a preference by Common Goldeneyes for nest boxes close to the water over those in forests (46–190 m from shore). They did not find any differences in predation rates between the two locations (Pöysä et al. 1997). Our boxes may have been more conspicuous than those in Pöysä et al.'s (1997, 1999) study, as they were highly visible in clearcuts. Unlike in British Columbia (Savard 1988, Evans et al. 2002), black bears (*Ursus americanus*) were not important predators, with only one box destroyed over the study. Other potential nest predators included red squirrel and marten (*Martes americana*). Mink (*Mustela vison*) were also numerous in the study area but it is unknown whether they can prey on birds or eggs in nest boxes; however we documented predation on Barrow's Goldeneye females and ducklings on two occasions in July 2002.

Numbers of breeding pairs of both Barrow's and Common goldeneyes increased. Our impact on local Barrow's Goldeneye productivity (Robert et al. 2006) may explain partially the greater increase of Common Goldeneye pairs over the course of the study. Goldeneyes have a strong breeding philopatry (Dow and Fredga 1983, Savard and Eadie 1989), so that local reproductive success is important for local population growth. The number of broods increased between 1999 and 2000, when nest box use increased from 1 to 30 boxes and hatching success was high. However, in subsequent years, increase in nest box use did not result in greater brood numbers. This was evident for Common Goldeneyes, especially in 2003 when the brood/pair ratio was only 15%. Pöysä and Pöysä (2002) showed that provision of nest boxes for Common Goldeneyes did not always result in greater productivity because of density dependence factors during nesting and brood-rearing. We believe that nest boxes could be used as a recovery tool for the eastern population of Barrow's Goldeneyes in areas where intensive forest exploitation may limit natural nest sites. However, their potential for increasing productivity may be limited by the availability of local brood rearing habitats.

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MOLT AND BODY MASS OF RED KNOTS IN THE EASTERN UNITED STATES

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ABSTRACT.—Red Knots (*Calidris canutus*) that spend winter in the southeastern United States are known to have been genetically separated from their congeners that migrate to Patagonian wintering grounds for about 12,000 years. We examined and documented differences between the two groups in their use of southward migration stopover locations, flight feather molt, fidelity to wintering zones, and differences in mass at southward migration stopover locations. Red Knots wintering in the southeastern United States do so consistently, and knots wintering in Patagonia have not changed to wintering in the southeastern United States. The two wintering groups have distinct differences in their nonbreeding season biology (e.g., migration strategies, chronology of pre-basic molt), and these differences have been maintained for decades if not millennia. *Received 24 August 2004. Accepted 22 July 2006.*

Red Knots (*Calidris canutus*), a Holarctic breeding shorebird, have a relatively large, albeit poorly-known breeding range in the Nearctic (Harrington 2001). There are at least two regions in the Western Hemisphere where relatively large numbers of Red Knots are known to spend their winter, one on the Patagonian coasts of Argentina and Chile (Patagonian-wintering knots), and the other (northern-wintering knots) ~9,500 km to the north, including areas in the southeastern United States (Morrison and Harrington 1992). Based on evidence of differing migration strategies and differential survival estimates for these two wintering groups, Harrington et al. (1988) questioned whether knots from the Patagonian and U.S. wintering regions were from different breeding groups with little genetic exchange. Buehler and Baker (2005) confirmed that Patagonian-wintering and northern-wintering knots have been genetically isolated for about 12,000 years. Little additional information is known about how these two groups differ in their biology.

The objectives of our study were to explore the possibility that Red Knots wintering in the U.S. differed from those wintering in Patagonia in flight-feather molt, movement of color-banded birds, plumages, and migration chronology. We tested the hypotheses that Patagonian and northern-wintering knots have developed distinctly different migrations as reflected in differences of their flight-feather molt, migration-related mass gain, principal migration stopover locations, as well as wintering locations.

METHODS

Study Areas.—We studied two regions used by knots during southward migration: Cape Cod and western Cape Cod Bay in Massachusetts, and the Altamaha River Estuary on the Georgia Atlantic coast. Sites in Massachusetts included Third Cliff Beach (42° 10′ N, 70° 43′ W), and Monomoy Island and South Beach in Chatham (41° 38′ N, 69° 58′ W). In Georgia we worked mostly on Wolf Island (31° 19′ N, 81° 17′ W), Little Egg Island Bar (31° 18′ N, 81° 16′ W), and Little St. Simons Island (31° 17′ N, 81° 16′ W). Additional observations were on the Florida west coast, principally between Bonita Springs (26° 24′ N, 81° 54′ W) and Honeymoon Island in Dunedin (28° 04′ N, 82° 50′ W).

Capture and Banding.—We captured knots using rocket and cannon nets placed at locations where flocks of knots gathered at high-tide roosts during the day. We used trained, volunteer crews to remove captured birds from nets to well-ventilated holding containers prior to processing. Standard, uniquely-numbered U.S. Federal bands and color bands were applied to tarsi and meta-tarsi in combinations to allow visual identifications of capture location and date. Birds were released at capture locations.

We used a rocket net in Massachusetts for capturing 1,363 adult Red Knots at Third Cliff

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Beach and Plymouth Beach (42° 59′ N, 70°, 39′ W) during July and August, 1980–1983. Birds were evaluated for flight feather molt, and body mass to the nearest gram. Birds were processed and released on site. We assigned age (adult or juvenile) based on plumage characters (Hayman et al. 1986). During August 2004 and 2005 we also collected information on flight feather molt by watching flocks through telescopes when wing-stretching is commonly seen, i.e., shortly before flocks depart high-tide roosts for foraging areas (BAH, pers. obs.), and by careful scrutiny of close-by knots in flight.

We used a rocket net to capture, color-mark, and release knots during January (n = 272 adults) and October (n = 99 adults) 1981 at Longboat Key (27° 20′ N, 82° 36′ W) on the west coast of Florida. Birds from all catches were evaluated for flight feather molt, and were weighed to the nearest 0.1 g using a triple-beam balance. Birds were processed and released on site. We did not use data from individuals less than 12 months of age, based on plumage characters (Hayman et al. 1986).

We captured 226 adult knots in Georgia using a cannon net set at three high-tide roosting locations in the Altamaha River Estuary (31° 18′ N, 81° 17′ W). We processed most catches at the capture location, taking measurements of mass to the nearest 1.0 g using a Pesola™ spring scale, and scoring the primary feather molt condition.

Migration Counts.—We used International Shorebird Survey (ISS) data collected between 1975 and 2004 to evaluate numbers of knots counted in the eastern United States between June and December. ISS project guidelines ask cooperators to count shorebirds at sites they choose three times a month during spring and autumn migration periods. Data evaluated for this study were those collected between 1 July and 31 December at sites on the Massachusetts coast (67 sites; 4,066 counts), the Georgia and South Carolina coast (16 sites; 415 counts), and the Florida coast (61 sites; 1,614 counts).

We began field study of knots in the Altamaha Estuary in Georgia in September 1998, and estimated numbers each year during September through 2003. We made no effort to estimate numbers systematically on regular schedules at other times of year, but collected counts as opportunity allowed.

Primary Feather Molt.—Knots have a sequential primary flight-feather molt starting with the innermost feather and moving centrifugally (Ginn and Melville 1983). This enables scoring molt stages using the Ashmole (1962) system where each of the 10 primary feathers on the right wing can score between 0 and 5 points, depending on age and growth stage. A knot with 10 new primary feathers would score 50, one where the molt had progressed about half way from inner to outer primary feathers would score ~25, and one with 10 old primary feathers would score 0. Old primary feathers are distinguishable from new feathers by fading and extensive wear whereas new feathers are darker (less faded) with little wear. We scored the molt on samples of knots captured in Massachusetts, Georgia, and Florida. We used one-way ANOVAs to compare score means between years within study sites, and among study sites.

Color-band Searches.—We searched through flocks of knots in Massachusetts, Georgia, and Florida to find color-marked individuals, recording whether they were those we marked in Georgia, or ones marked by other researchers in Delaware Bay or South America. We used Chi-square analysis to compare the relative frequencies with which we found knots from these three banding origins.

Body Plumage Evaluation.—We recorded body plumage appearance of adult knots in Georgia, assigning scores ranging between 1 (complete basic plumage) and 5 (complete alternate plumage). These data were from knots randomly selected (n = 143) from flocks during studies of foraging birds on tidal flats close to our capture locations. Our samples in Massachusetts (n = 346) and Florida (n = 225) were from photographs of flocks taken at our capture locations. The plumages were scored as between 1 and 3 or between 4 and 5 because only partial views were possible from photographs. Results of statistical evaluations were considered significant at $P \leq 0.05$.

RESULTS

Autumn Migration Counts.—Peak counts of southward passage Red Knots in Massachu-

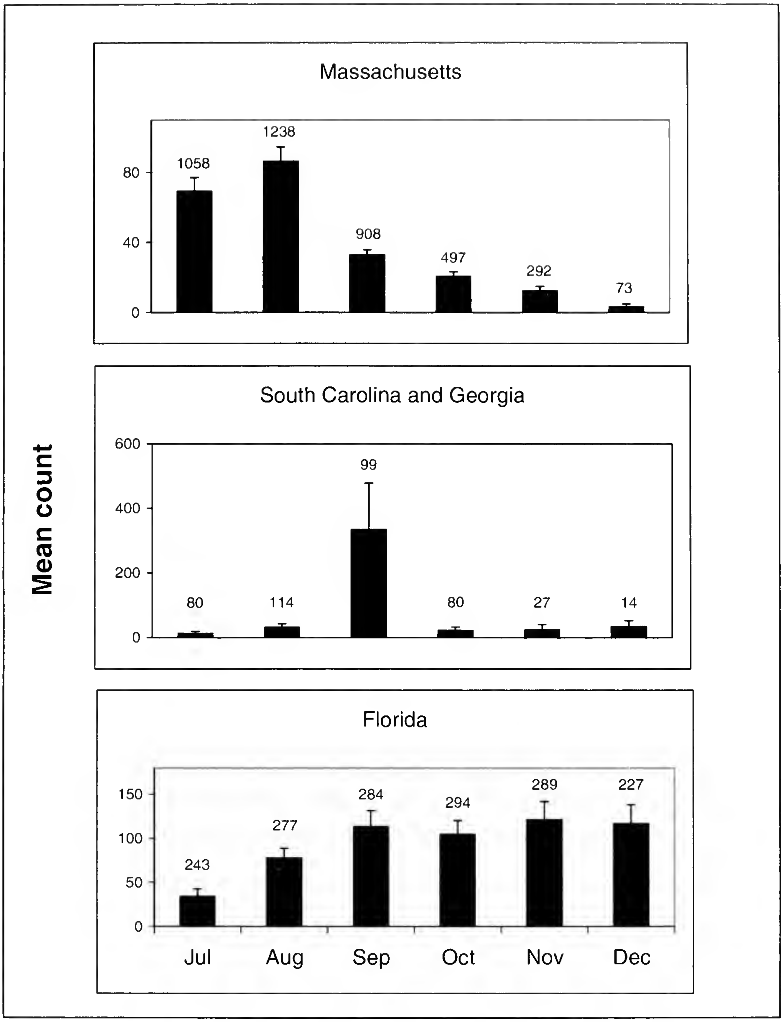

FIG. 1. Mean numbers (±1 SE) of Red Knots counted between July and December by the International Shorebird Surveys (ISS).

setts were during the first third of August, well before peak numbers were counted on the South Carolina-Georgia and Florida coasts (Fig. 1). We did not document the full seasonal chronology of the knot passage in Georgia because we were present only during September. However, by canvassing a number of visitors and occasional visits by BW and BAH, we believe the general pattern was that numbers increased during August, reached peak abundance during late September, and declined during October (Fig. 1). Our separate counts at the Altamaha Estuary during September indicated that numbers of knots varied considerably between years with maxima ranging from 5,000 (1999) to 10,000 (2001) birds.

Sightings of Color-banded Birds.—The information on the numbers of knots on the Massachusetts and Georgia coasts does not identify whether the knots visiting the Massachusetts coast were also visiting the Georgia coast. We believe that most knots transiting through Massachusetts during southward migration have South American destinations, and that most of those transiting through the Georgia stopover are enroute to U.S. or other northern wintering areas. We used resightings

TABLE 1. Numbers of Massachusetts and Georgia sightings during southward migrations (2003–2004) of Red Knots color-banded in either Georgia or South America.

	Banded in	
Resighted in	Georgia	South America
Georgia	82	9
Massachusetts	5	77
Florida	60	0

of color-banded knots at both locations in 2003 and 2004 to examine use of the Massachusetts and Georgia stopover locations in two ways: (1) the relative resighting frequencies of knots marked in Georgia and seen in Massachusetts, and (2) the relative resighting frequencies of Red Knots marked in South America and seen in Massachusetts as compared to Georgia. This comparison (Table 1) shows that substantially higher proportions of the knots transiting through Massachusetts versus Georgia have South American destinations.

We also compared the relative frequencies with which knots marked in either Georgia or South America were seen during winter (Nov–Feb 2003–2004) on the west coast of Florida, i.e., within the range of the northern wintering group. These results (Table 1) show that many of the knots transiting the Georgia migration stopover area during September have winter-ground destinations on the Florida west coast. The results also indicate that some unknown, but small, fraction of knots transiting the Georgia stopover have South American winter-ground destinations. This was confirmed by sighting a small number of the thousands that had been color-banded in Patagonia.

Plumage.—During July and early August in Massachusetts, virtually all of the 346 adult knots whose plumage molt we scored from photographs had mostly alternate body plumage (scores between 4 and 5, $n = 332$). Few had actively molting body plumage feathers, and it appeared the pre-basic molt had begun but became arrested north of (or possibly in) Massachusetts. The few (i.e., low hundreds) of adult Red Knots remaining in Massachusetts between late August and October had progressively greater amounts of basic plumage, and were in virtually complete basic plumage by October.

Most of the adult knots at the Altamaha Estuary, Georgia were in predominately basic plumage by early September (Fig. 2), and more than half had attained virtually complete

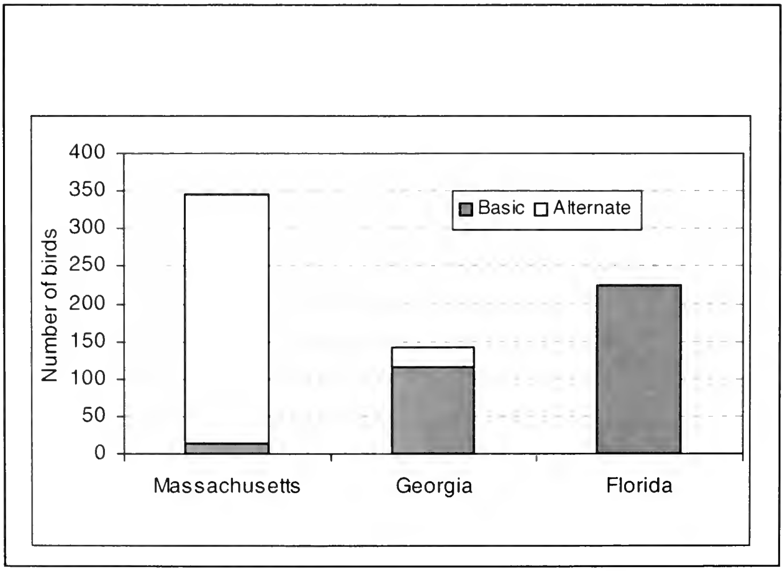

FIG. 2. Plumages (mostly alternate or mostly basic) of adult Red Knots in Massachusetts (Jul–early Aug), Georgia (Sep), and Florida (Oct).

basic plumage (i.e., the pre-basic molt was substantially more advanced than in Massachusetts). In Florida, during both October and January, virtually all adult knots were in basic plumage.

Primary Feather Molt.—We checked the primary flight feather molt in 1,363 adult knots captured on western Cape Cod Bay, Massachusetts during July and August, 1980–1983; all but two were prior to 13 August, after which date numbers of knots declined rapidly. We found no flight-feather molt among these knots.

In contrast to the above, BAH and Jake Walker found primary feather molt in 99 of 610 adult knots they checked on eastern Cape Cod during 2004 and 2005. Many of these birds appeared to be in a first basic plumage (dorsal body feathers substantially faded, with primary feather tips faded and heavily worn). In contrast, only one of 80 knots ($\chi^2 = 10.95$, $P < 0.001$) checked on western Cape Cod Bay (where banding occurred 1980–1983) showed primary feather molt.

We had sufficient captures in Georgia during September 2000–2002 to evaluate stages of primary feather molt in adult knots. We found no differences (ANOVA, $F_{2,194} = 0.72$, $P = 0.49$) of mean scores between years among knots actively or recently having completed (score 50) molt, and combined years for analysis. The average primary molt score of knots with actively growing feathers was 34.8 ($n = 171$, including 7 that were not weighed), indicating the typical molt had progressed from primary number 1 to primaries 6–8. There were some individuals ($n = 5$) with scores below 20 (involving primaries 1–4). In addition, others had recently completed the primary feather molt (score = 50, $n = 19$), and a few had 10 old primary feathers (score = 0, $n = 7$).

All but one of the 272 knots we captured in January 1981 in Florida had all new and fully grown primary flight feathers. Most knots (90 of 99 adults) on 10 October 1981 had growing primaries: the average score among 90 adults that were molting was 40.2 ± 0.53. We compared this October value to the mean value of a single group of 72 (score mean = 34.7 ± 0.8 SE) captured at Altamaha Estuary, Georgia on 11 September 2001 (restricted to adults having active primary feather molt). The Florida mean molt score from October was higher (ANOVA, $F_{1,160} = 22.\ 2$, $P < 0.01$) than the mean score from mid-September in Georgia.

TABLE 2. Body mass of adult Red Knots at different stages of primary feather molt during September 2000–2003 on the Georgia coast.

Groups	*n*	Mean weight (g)	SD
Primary score 0	7	141.0[a]	12.0
Scores 7–49	169	132.1	10.4
Scores 50	19	149.6	22.6

[a] Lower than the Massachusetts mean of 161.7 g in July/August.

Body Mass.—The average mass of captured knots ($\bar{x} = 161.06 \pm 0.64$ SE, $n = 1{,}341$) in Massachusetts during July–August (1980–1983) was greater (ANOVA, $P < 0.01$) than for knots captured after August in Georgia ($\bar{x} = 134.4 \pm 0.9$, $n = 199$) or Florida during October ($\bar{x} = 124.9 \pm 0.7$, $n = 99$) and January 1981 ($\bar{x} = 137.1 \pm 0.7$, $n = 145$). Mean body mass of birds caught in Massachusetts on different dates generally increased until principal migration departures on ~10 August. For example, mean values were 132.3 g ± 1.2 SE ($n = 161$) on 26 July 1983, 153.0 ± 1.2 on 1 August 1984 ($n = 146$), and 185.1 ± 1.3 ($n = 132$) on 7 August 1980.

Body mass of Red Knots in Georgia was lower (ANOVA, $F_{2,196} = 5.59$, $P = 0.004$) in 2001 versus 2000 or 2002. The knots during 2001 were foraging principally on sodbanks after their favored local prey (bivalves in the genera *Mulinea* and *Donax*) had largely disappeared. Weights of knots from Georgia were slightly more variable than at the Massachusetts and Florida sites. The annual variation of mass in Georgia was apparently related to annual differences in food resources.

We combined data from all years to compare the mean body mass of knots that were not molting primary flight feathers to those that that were molting. Those molting were lighter (ANOVA, $F_{2,194} = 34.8$, $P < 0.001$) than knots that were not molting (Table 2).

DISCUSSION

We conclude from our data (Table 3) that Red Knots in Massachusetts and Georgia represent groups with distinctly different wintering destinations. Most that passage south

TABLE 3. Chronology and molt of Red Knots migrating south through Massachusetts and Georgia.

	Massachusetts	Georgia/Florida
Chronology	Depart mid-Aug	Depart in Oct
Principal months for primary feather molt	Nov–Jan in Patagonia	Aug–Nov in Georgia and Florida
Weight change	Rapid body mass gain in Jul/Aug	Little or slow mass gain in Sep
Body plumage molt	Alternate plumage in Aug, with arrested pre-basic molt	Little alternate plumage remaining in Aug, ongoing pre-basic molt
Color-banded birds from South America	Many with bands from South American wintering areas	Few with bands from South American wintering areas
Color-banded birds from Georgia	Few with bands applied during Sep in Georgia	Many in Florida banded during Sep in Georgia

through Massachusetts migrate to Patagonia, whereas most of those in Georgia winter in the Northern Hemisphere including the southeastern U.S. These results support earlier speculation (Harrington et al. 1988) and recent genetic studies (Buehler and Baker 2005) which show the two wintering areas are populated by separate groups of knots.

Counts During Autumn and Winter.—Numbers of southward migrating Red Knots increase on the Massachusetts coast during the second half of July and decline after reaching peak levels in the first or second third of August. The decline in Massachusetts (mid-Aug) occurs at about the same time that knots begin to appear in northern South America (Spaans 1978).

Our information from color banding as well as previous information (Harrington et al. 1988) shows that most knots on the Massachusetts coast during early August travel by direct, over-ocean flights to South America (Harrington 2001). It is possible that some knots departing Massachusetts follow the U.S. Atlantic coast southwards, comprising a small fraction of the knots that visit southeastern states.

The increase in numbers of knots in the southeastern U.S. begins in late July/early August as in Massachusetts. However, numbers in Georgia do not decline in August, but remain stable or perhaps continue to increase slowly between August and October, after the early October arrival dates of knots in Argentina (Harrington 2001). Knots marked in Georgia are commonly found on the Florida west coast, a contrast to their numbers found in Massachusetts (Table 1).

Plumage and Primary Feather Molt.—Red Knots passing through Massachusetts during July and August have a predominately alternate plumage. Active pre-basic molt of body plumage in Massachusetts becomes arrested, and molt does not resume prior to the principal migration departure during mid-August (Morrison and Harrington 1992). The small numbers of adults that remain in Massachusetts after mid-August possibly represents birds that are enroute to southeastern U.S. states.

Most Red Knots in Georgia during August/September have ongoing pre-basic molt as evidenced by plumages changing from largely alternate to largely basic (Fig. 2). Most adult knots in Georgia also have active primary feather molt (Table 2), with the majority having molted slightly more than half of the primary feathers by mid-September.

Body Mass.—The average body mass for Red Knots in Georgia was greater in birds that were not molting flight feathers than in birds that were molting flight feathers. We interpret these data as evidence they were preparing for a long-distance, non-stop migration flight (Gudmundsson et al. 1991). An alternative idea is that non-molting knots were heavier simply because they were not molting, i.e., as a consequence of a presumed close relationship between active primary feather molt and low body mass (Lindström et al. 1994). However, Holmgren et al. (1993) found no relationship between body mass and presence or absence of flight feather molt in Dunlin (*Calidris alpina*).

It is generally believed that shorebirds do not gain mass unless preparing for migration (Burns and Ydenberg 2002) or for cold winter weather (Dugan et al. 1981). The mean mass of 597 Red Knots wintering in Tierra del Fuego, Argentina during February, when primary feather molt was presumably completed, was 126.8 g (Baker et al. 1996). This average is ~14 g less than the average mass in the small sample of knots having molt scores of 0 in Georgia, and ~22 g less than the average for the Georgia knots that had all new primary feathers. Thus, there is insufficient evidence to show that knots without active primary feather molt would necessarily weigh more than knots that do have active primary feather molt.

CONSERVATION IMPLICATIONS

Our results confirm there are at least two distinct wintering groups of Red Knots in the Western Hemisphere. However, we do not know the relative proportions that historically used Delaware Bay during spring. The Patagonian wintering group, once estimated to be 100,000–150,000 knots (Morrison and Harrington 1992), is undergoing an alarming population decline, and now number fewer than 20,000 birds (Morrison et al. 2004). The population status of the northern-wintering group of knots is being assessed, but early evidence (Harrington et al. in prep) does not suggest it is declining. If the population decline of the knots that winter in Patagonia is linked to Delaware Bay food resources, and if the same was true for northern-wintering knots, then we would expect to see commeasurable declines in numbers of the northern-wintering knots. Ongoing studies suggest an explanation for this 'disconnect' is forthcoming.

Earlier work (Harrington et al. 1988) suggests the northern-wintering group of Red Knots were proportionately less common on Delaware Bay than the Patagonian-wintering group. Recent (2003–2004) feather isotope analyses (Atkinson et al. 2005) suggest that a third of the knots using Delaware Bay during northward migration are from the "northern" wintering area. This suggests that a significant proportion of the northern-wintering knot population migrates through Delaware Bay in spring, and/or that the "northern" group has a substantially larger population size than we have estimated.

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HAIRY WOODPECKER WINTER ROOST CHARACTERISTICS IN BURNED PONDEROSA PINE FOREST

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ABSTRACT.—Winter roosts afford escape from extreme climatic conditions, reduce heat and energy loss, and provide protection from predators for North American woodpeckers. We monitored the use and characteristics of 12 winter roosts used by nine radio-marked Hairy Woodpeckers (*Picoides villosus*) in ponderosa pine (*Pinus ponderosa*) forests of northern Arizona that had experienced wildfire in 1996 and 2000. Roost trees were larger in diameter than 95% of non-roost trees and on average 2.5 times larger within burned areas of similar severity. Roost trees were within patches less dense than 95% of measured patches across study sites, which were on average 1.5 times as dense. Two-thirds of roost trees were created by fire and were smaller than those created by other means. Six birds each used one roost and three males each used two roosts. Two-thirds of the roosts were outside or on the edge of estimated home ranges. Maximum straight-line distances traveled, from roost to farthest point of home range, were >1 km for 8 of 9 birds. Woodpeckers have a significant role in providing cavities for secondary cavity nesters. Thus, understanding habitat requirements for winter roosts could provide managers with essential tools to maintain or enhance populations of this species. *Received 19 October 2005. Accepted 14 July 2006.*

Snags are the principal substrate for both nesting cavities and winter roosts for primary cavity nesters in coniferous forests (Hutto 1995) and snag availability may limit population size (Newton 1994, Schepps et al. 1999). While information has been collected on characteristics of cavities used for nesting (Hutto 1995, Saab et al. 2002), little has been collected on winter roost trees and their use, even though winter is a critical period for resident birds (but see Pileated Woodpecker [*Dryocopus pileatus*], e.g., Bull et al. 1992, Kellam 2003). Low-temperatures, high winds, and precipitation increase metabolic costs (Walsberg 1986, Cooper 1999). Additionally, while shorter days decrease time available for foraging, food resources become limited (Askins 1981). This results in an increased proportion of time birds forage to gain adequate food resources, which leads to increased predation risk (Houston and McNamara 1993). Roost holes alleviate some of these pressures by providing insulation (Askins 1981, 1983), reduced exposure to wind and precipitation, and an increase in nightly energy conservation, thereby reducing time necessary for foraging (Conner 1975, Stauffer and Best 1982, Li and Martin 1991, Cooper and Swanson 1994). Roosts also provide protection from both nocturnal and diurnal predators (Dolby and Grubb 1999).

Fire changes the distribution and abundance of snags available for winter roosts and alters the rate of snag turnover, depending upon the length of inter-fire intervals (Newton 1994). In northern Arizona, ponderosa pine (*Pinus ponderosa*) forests historically experienced low-severity fires every 2–12 years and fires ranged from several hundred to several thousand hectares in size (Covington et al. 1997, Fulé et al. 2003). Within these fires, small patches of snags were generated in high frequency across the landscape (Fulé et al. 2004). As a consequence, this system could have had the potential for relatively rapid snag turnover (Newton 1994). More recently, fire suppression and logging have altered historical fire regimes and have led to dense stands of small-diameter trees that can support large wildfires. Although fire often attracts primary cavity nesters due to an increase in bark- and wood-dwelling insect prey (e.g., Blackford 1955, Koplin 1969, Hutto 1995, Murphy and Lehnhausen 1998), little information exists about where these birds roost relative to burned and unburned areas or the characteristics of trees used as roosts.

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Winter roosts are important for over-winter survival, which ultimately affects the number of available breeders entering subsequent nesting periods. Thus, information on roost characteristics used by woodpeckers in burned ponderosa pine forests may help managers make guided decisions to conserve these important primary cavity-nesting species. We present roost characteristics, use, and location relative to home ranges for nine radio-marked Hairy Woodpeckers (*Picoides villosus*) monitored for a study of their winter ecology (Covert-Bratland et al. 2006). We provide baseline data, methods for future investigation, and several hypotheses to direct future research.

METHODS

Study Area.—During winter 2002–2003, we studied Hairy Woodpeckers in monotypic ponderosa pine forests of northern Arizona burned by three different wildfires. In 1996, the Horseshoe and Hochderffer wildfires burned 10,022 ha in the Coconino National Forest 48 km northwest of Flagstaff, Arizona (35° 37′50″ N, 111° 79′62″ W). Because these fires were adjacent to each other, we treated them as one site. The Pumpkin fire burned 5,973 ha in May 2000, in both the Coconino and Kaibab National forests (35° 37′45″ N, 111° 90′79″ W) adjacent to the earlier Horseshoe-Hochderffer fires. Thus, at the time of our study, the sites represented burns that were 7 and 3 years of age, respectively. Fires burned with varying intensity, resulting in a mosaic of high- and moderate-burn severities and unburned areas across the landscape. We sampled in high-severity areas, those where fire reached the forest crown and killed 99% of ponderosa pine, and moderate-severity areas, those where low-intensity surface-fires resulted in <10% tree mortality (adapted from Dwyer and Block 2000).

Other woodpecker species in the study area during winter, in decreasing relative abundance, included Northern Flicker (*Colaptes auratus*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), Three-toed Woodpecker (*Picoides tridactylus*), and Downy Woodpecker (*P. pubescens*) (WMB, unpubl. data). These species were relatively rare, as the relative abundance of each compared to that of the Hairy Woodpecker (with the Hairy Woodpecker as 1) was 0.33, 0.05, 0.03, and 0.01, based on average detections per point-count station. Of these woodpeckers, the Downy Woodpecker is considered a weak excavator (Martin et al. 2004) and the Williamson's Sapsucker roosts in natural or secondary cavities (Dobbs et al. 1997).

Field Methods.—We used radio telemetry to locate and monitor Hairy Woodpecker winter roosts. Between 18 October and 18 December 2002, we searched for Hairy Woodpeckers over 5,000 ha of our study area and mist-netted nine individuals using tape playback calls of Hairy Woodpecker and Northern Pygmy-owl (*Glaucidium gnoma*). Each bird was individually marked with a federal band and two color bands. Additionally, we attached a BD-2, 1.7 g, 18-cm whip-antenna, 14-week-lifespan, transmitter (Holohil Ltd., Carp, Ontario, Canada) to the central two rectrices with epoxy glue and secured with dental floss on the body of the transmitter and at 2 15-cm intervals down the antennae. Transmitter mass was approximately 3% of the bird's body mass.

We located roost cavities of radio-marked birds from 22 October 2002 to 14 March 2003 between 1700 and 2100 hrs MST. Each individual's roost tree was monitored a minimum of four times throughout the season at regular intervals of approximately two weeks. Cavities used were located using radio telemetry, or, if more than one cavity entrance was present in the area of strongest transmission, observers would return the following morning 15 min before sunrise to watch the bird emerge. This process was repeated twice for cavity verification.

Structural and burn characteristics of the roost tree, patch, and surrounding forest were measured. For each roost tree, we recorded: (1) roost tree location (UTM using Garmin 12 Global Positioning System [GPS] units); (2) roost tree species, its likely cause of death, and the tree's burn severity (unburned, moderate, or high), diameter at breast height (dbh), percent retained bark, and whether it was topped (upper portion of the trunk broken off); (3) number of cavities in the roost tree and which were occupied by the Hairy Woodpecker; and (4) height and orientation of each cavity. We also recorded data for the patch around the roost tree: (1) burn severity within a 25-m radius; (2) distance to nearest patch of alternate severity (e.g., if a roost was in an unburned patch where was the nearest patch of moderate- and high-severity burn) using the roost tree as the point from which measurements were taken; (3) tree density; and (4) mean patch dbh. We calculated patch tree density using the point-center quarter method by averaging distances from the roost tree to the four nearest trees ($\geq$2 m in height) in each cardinal quadrant (Cottam and Curtis 1956). Similarly, we calculated the mean patch dbh by averaging the dbh measurements of the same four trees. We then compared that mean to the dbh of the roost tree.

We compared roost tree and patch measurements to the mean of each variable measured within the surrounding ponderosa pine system studied by placing randomly oriented vegetation grids (100 × 100 m grid cells) over study sites in ArcView 3.2a (Environmental Systems Research Institute 2004). Thus, we could find the exact location of each grid-intersection in the field using GPS. At each intersection (n = 338), we selected the nearest tree to serve as the random center-tree and within each cardinal quadrant selected the tree closest to the center tree to measure tree density and mean patch dbh. We recorded the center tree's species, burn severity, dbh, percent-retained bark, and whether it was topped. We measured the distance to all trees in each cardinal quadrant and their respective dbh. We used Wilcoxon signed ranks test to compare roost tree dbh, density, and patch dbh to the mean of each variable in the surrounding forest of the same age and burn severity. We used Mann-Whitney tests to compare the dbh and number of cavities in fire-killed snags versus snags created by other means. Mean orientation and significance of cavity orientation for all cavities were calculated using Rayleigh's test (Zar 1999:616). All tests were performed using SPSS (SPSS, Inc. 2002). Statistical significance was set at α = 0.05 and means are presented ± SE.

The youngest post-burn age of a high-severity roost tree in which Hairy Woodpeckers would create a cavity was based on observations of cavity excavation in the younger Pumpkin fire. We were able to monitor cavity creation one year prior to collecting roost data, which was taken only during the second year of the overall study (Covert-Bratland et al. 2006). During foraging observations, which were conducted by systematically searching 300-m belt-transects 2–5 times during winter 2001–2002 and 2002–2003, any observation of a Hairy Woodpecker excavating a cavity was noted. The total number of excavations for two seasons is presented for fires representing 2 and 3 years post-wildfire.

Location of Roosts Relative to Diurnal Home Range.—We calculated the distance from the roost to several points within each individual's diurnal home range (Covert-Bratland et al. 2006). We defined diurnal home range as the area used for daily foraging and other activities between 0800 and 1600 hrs excluding travel to and from roost sites. We used both the 85% fixed-kernel (pre-hoc smoothing factor) and minimum convex polygon (MCP) methods calculated with "Animal Movement" extension (Hooge and Eichenlaub 1997) in ArcView 3.2a (Environmental Systems Research Institute 2004) to estimate home ranges. We classified the location of each roost relative to the diurnal home range (Covert-Bratland et al. 2006) as either inside (within the diurnal home range but not within 50 m of the edge), on the edge (within ± 50 m of the 85% contour), or outside the home range (>50 m from the 85% contour edge, in which case the distance was calculated as below).

We found no information on distances traveled by Hairy Woodpeckers in the literature to compare to distances traveled in this study. We established baseline movement distances for future research by calculating the distance from each bird's roost tree to (1) the closest point on the 85% contour interval, (2) the arithmetic mean of the diurnal home range estimated by the fixed-kernel method, and (3) the farthest known diurnal foraging location. We used the "Animal Movement", "X-tools" (Environmental Systems Research Institute 2004), and "Weighted Mean" extensions (Jenness 2004) in ArcView 3.2a to calculate these distances.

RESULTS

We located and measured 12 Hairy Woodpecker roost trees during winter 2002–2003 (Tables 1, 2). Three females and three males each used one roost tree during the period

TABLE 1. Characteristics of winter roost trees and roost-tree patches (as defined by point-center quarter) used by Hairy Woodpeckers in ponderosa pine forest burned in the Pumpkin (3 years post-wildfire) and Horseshoe/Hochderffer (7 years post-wildfire) wildfires, Coconino National Forest, Arizona, during winter 2002–2003. Characteristics of roost trees and patches are given first, followed by the mean ± SE of trees and patches present in the surrounding forests within the corresponding burn age and burn severity.

Burn age	Gender	Bird	Roost tree species[a]	Snag type[b]	Roost tree burn severity[c]	Patch burn severity	DBH (cm)	Surrounding DBH (cm)	Tree density	Surrounding tree density	Patch DBH (cm)	Surrounding patch DBH (cm)
3	F	894	PIPO	S	UNB	UNB	88.0	22.5 ± 1.8	0.23	0.44 ± 0.06	19.6	21.1 ± 1.5
	M	100	PIPO	FK	HIGH	MOD	72.2	17.4 ± 1.3	0.14	0.28 ± 0.03	32.1	29.1 ± 1.1
		951a	PSME	FK	HIGH	HIGH	60.8	17.4 ± 1.3	0.27	0.44 ± 0.03	34.1	19.9 ± 0.1
		951b	POTR	FK	HIGH	HIGH	24.6	17.4 ± 1.3	0.44	0.44 ± 0.03	9.5	19.9 ± 0.1
7	F	182	PIPO	FK	HIGH	MOD	27.9	24.5 ± 1.0	0.15	0.21 ± 0.01	38.3	28.7 ± 0.6
		990	PIPO	FK	HIGH	HIGH	45.1	24.5 ± 1.0	0.14	0.19 ± 0.01	29.6	24.6 ± 0.6
	M	209a	PIPO	S	MOD	MOD	66.9	30.5 ± 1.2	0.11	0.21 ± 0.01	21.1	28.7 ± 0.6
		209b	PIPO	BBK	MOD	MOD	89.0	30.5 ± 1.2	0.21	0.21 ± 0.01	27.6	28.7 ± 0.6
		293	PIPO	CF	MOD	MOD	45.5	30.5 ± 1.2	0.18	0.21 ± 0.01	34.6	28.7 ± 0.6
		835	PIPO	FK	HIGH	HIGH	55.0	24.5 ± 1.0	0.11	0.19 ± 0.01	32.5	24.6 ± 0.6
		910a	PIPO	FK	HIGH	HIGH	50.3	24.5 ± 1.0	0.13	0.19 ± 0.01	17.3	24.6 ± 0.6
		910b	PIPO	FK	HIGH	HIGH	41.0	24.5 ± 1.0	0.18	0.19 ± 0.01	30.3	24.6 ± 0.6

[a] PIPO = *Pinus ponderosa*, ponderosa pine.
PSME = *Pseudotsuga menziesii*, Douglas-fir.
POTR = *Populus tremuloides*, quaking aspen.
[b] S = Snag, pre-fire.
FK = Fire killed ponderosa pine.
BBK = Bark beetle killed tree.
CF = Cat face, dead portion in live PIPO tree, likely caused by lightning.
[c] UNB = unburned.
MOD = moderate.
HIGH = high.

TABLE 2. Winter roost tree use and location relative to diurnal home range attributes (fixed kernel estimate) of Hairy Woodpeckers in the Pumpkin (3 years post-wildfire) and Horseshoe/Hochderffer (7 years post-wildfire) wildfires, Coconino National Forest, Arizona, winter 2002–2003. Distances are from the roost tree to (1) the nearest point along the edge of the 85% kernel contour (negative values indicate roost trees inside the home range), (2) the center of the home range calculated using arithmetic mean, and (3) the farthest known foraging location of a bird within its diurnal home range.

Burn age	Gender	Bird	Nights used of total observed	Distance to nearest high-severity patch (m)	Distance to nearest moderate-severity patch (m)	Distance to HR[a] edge (m)	Distance to HR center (m)	Distance to farthest location in HR (m)
3	F	894	6/6	200	20	1,019.5	1,346.3	1,618.0
	M	100	5/5	250	—	205.8	374.9	565.3
		951a	1/5	—[b]	90	0.0	498.2	1,524.2
		951b	4/5	—	175	0.0	298.0	1,006.0
7	F	182	4/4	1,207	—	−373.3	500.5	2,045.0
		990	5/5	—	15	−379.5	1,007.0	2,306.3
	M	209a	4/5	25	—	5.7	159.9	1,446.8
		209b	1/5	450	—	140.1	561.8	1,427.9
		293	5/5	200	—	161.1	376.9	1,375.6
		835	6/6	—	25	40.2	377.8	1,302.6
		910a	4/5	—	15	−338.3	689.4	2,075.2
		910b	1/5	—	18	−217.3	594.0	1,936.3

[a] HR = home range.

[b] Indicates roost tree is within column severity.

monitored, and three additional males used two different roosts (Table 2). Eight roost trees were killed by fire, 3 in the 3-year-old burn and 5 in the 7-year-old burn. These 8 roost trees were categorized as high-severity and the majority (6 of 8) was within high-severity burned areas. Of those in high-severity areas, 4 of 6 were within 25 m of the edge of a moderate-severity patch. Roost trees killed by other means were in unburned areas that had not experienced fire since the roost was created, were within moderate-severity areas, and/or were killed by a secondary mortality agent after fire injury. Most trees retained the majority (mean = 82 ± 6.8%, range = 31–100%) of their bark. All trees leaned less than 5% from vertical and all but three trees were topped. Those not topped were either still alive or recently killed, precluding the decay process that would lead to topping.

Roost trees ranged in size from 24.6 to 89 cm dbh (mean = 55.5 ± 6.0 cm), and 9.5–31 m in height (mean = 18.9 ± 2.7 m). Roost trees used by Hairy Woodpeckers were on average 2.5 times larger in dbh than those in the surrounding forest within the same burn and age class ($Z = -3.1$, $P = 0.001$). Fire-killed trees were substantially smaller in dbh (mean = 47.1 ± 5.7 cm) than roost trees created by other means (mean = 72.3 ± 10.3 cm, $Z = -1.9$, $P = 0.03$). Regardless of burn age or severity, the mean density of trees surrounding the roost tree was substantially less than of trees in the surrounding forest ($Z = -3.1$, $P = 0.001$). The mean patch dbh of the trees closest to the roost tree was variable and did not differ from that of trees closest to a random tree in the surrounding forest ($Z = -0.8$, $P = 0.43$). Roost tree dbh was larger (6–69%) than the patch mean for all but one roost tree.

All roost trees had multiple cavities (range = 2–10, mean = 4.8 ± 0.8), however, each bird used only one cavity repeatedly and most appeared to be newly created that winter ($n = 11$). Fire-killed roost trees tended to have fewer cavities on average (mean = 3.9 ± 0.79) than snags created by other mortality factors (mean = 6.7 ± 1.44, $Z = 1.63$, $P = 0.051$). Cavity entrances ranged from 1.8 to 18.4 m (mean = 8.0 ± 1.2 m) above the ground corresponding to 9–85% of the total tree height. Five cavity entrances were under branches. The majority of roost hole entrances ($n = 9$, Fig. 1) faced north-northeast (mean angle = 21.27, angular dispersion 56.1°, $Z = 2.68$, $P = 0.006$) whereas those that faced south or west were on northeast slopes or in roost trees surrounded by dense unburned forest. Hairy Woodpeckers were observed excavating cavities 5 times in burned areas 2 years post-wild-

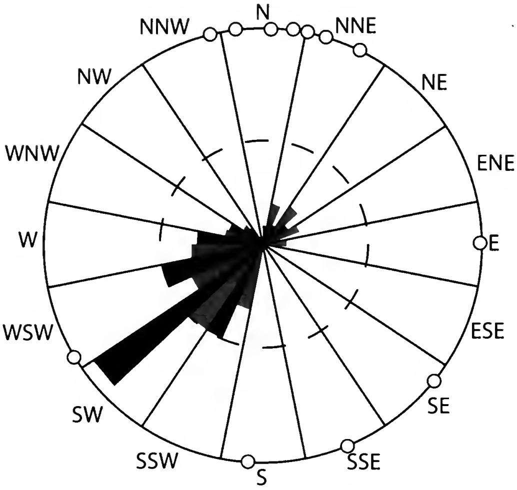

FIG. 1. Orientation of roost entrance holes (open circles) relative to southwest prevailing winds (Acker 2003) used by Hairy Woodpeckers within the Horseshoe/Hochderffer and Pumpkin burns, Coconino National Forest in northern Arizona during winter 2002–2003.

fire and 21 times in burned areas 3 years post-wildfire.

Only males changed roost trees during the study (Table 2). One male moved to a secondary roost within two weeks prior to the first week of December, whereas the other two males switched during the last week of February, only several weeks prior to nesting initiation. Two males moved to secondary roosts that were 100–200 m closer to their home range centers, whereas one moved to a location 400 m away. All three secondary roosts were closer (mean = 225.3 m) to the farthest foraging locations for those individuals, or the farthest extent of their home range.

Four roosts were outside of the calculated home range (fixed kernel method), four were within 50 m of the edge, and four were inside the home range (Table 2). The mean distance to home range boundaries for roost trees outside the home range, was 381.6 ± 213.1 m (range = 140.1–1,019.5 m). Three roosts were outside of the diurnal home range (MCP method), three were on the edge, and six were inside (Fig. 2). Distances from the roost tree to the center of the kernel home range averaged 565.4 ± 94.3 m (range = 159.9–1,346.3 m). The mean distance from roosts to the home range center for birds occupying 3-year-old burned areas was 629.4 ± 242.5 m versus 533.4 ± 88.9 m for birds occupying older burns, even though home range sizes for birds in older burns were larger.

DISCUSSION

All roost cavities were either in dead trees (snags) or within dead tissue in live trees, suggesting that Hairy Woodpeckers limited cavity excavation to dead tissue. Ponderosa pine has high volumes of sapwood relative to rot-resistant heartwood (Lowell and Cahill 1996). This ratio facilitates decay in portions of the tree of greatest volume, where cavities can then be excavated (Bull et al. 1997). Sapwood without rot is relatively hard and resists excavation (George and Zack 2001), making tree decay prior to excavation critical. Woodpeckers spend considerable energy excavating cavities and factors that decrease wood hardness and density would decrease energy expenditure needed to make cavities (Conner et al. 1976, Schepps et al. 1999). This would be especially beneficial during winter when energy requirements for survival are elevated (Walsberg 1986).

Most winter roosts were in fire-killed trees, in areas that had experienced high-severity wildfire, and in 3- and 7-year-old burned areas. Hairy Woodpeckers also used snags present before fire, indicating that roosts may be used after a fire if the roost tree and cavity are not too damaged. Historically, fire was the primary disturbance agent within northern Arizona's ponderosa pine forests (Covington et al. 1997), and could have generated small patches of snags in high frequency across the landscape (Fulé et al. 2004). Fire generates snags both directly by killing trees, and indirectly by increasing the susceptibility of surviving trees to secondary mortality agents that exploit the initial fire-caused injury (Salaman 1934, Flanagan 1996, McHugh and Kolb 2003).

Cavities were associated with snags >4 years old in studies of non-fire-killed roost trees. Scott (1978) found that most non-fire killed snags used by cavity nesters were at least 6 years old in northeastern Arizona and

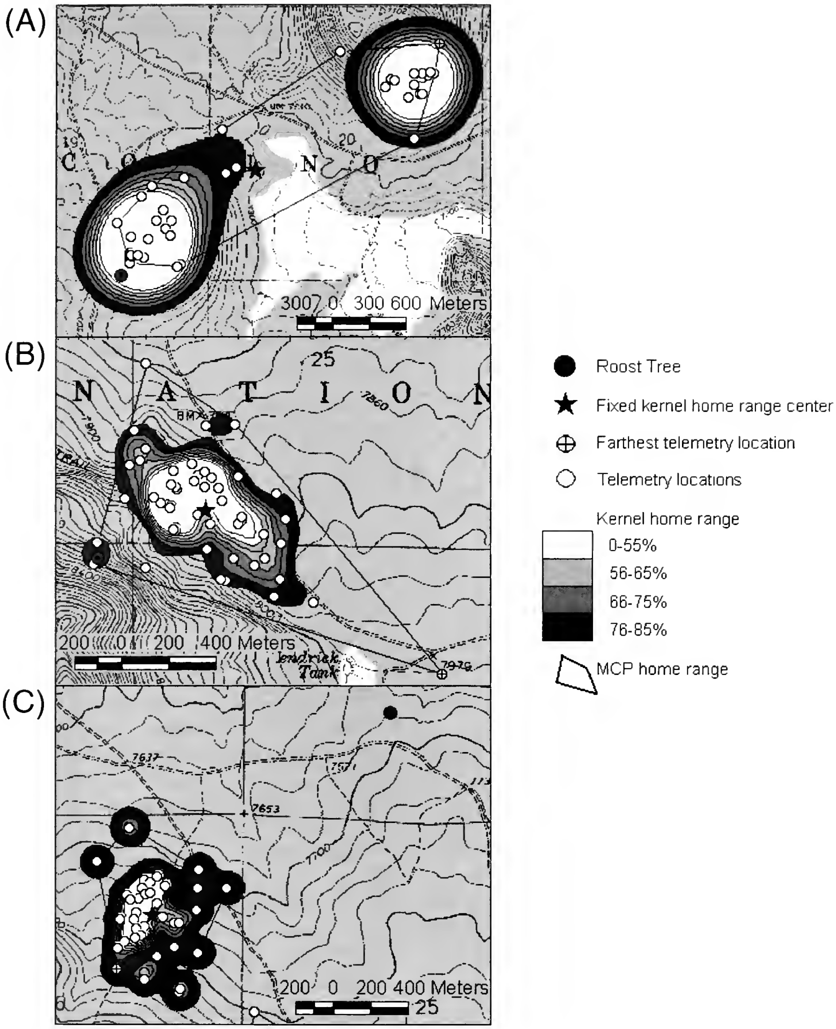

FIG. 2. Three Hairy Woodpecker winter roosts and home ranges as estimated by the 85% fixed kernel and minimum convex polygon (MCP) methods. Home range centers were estimated by the arithmetic mean and the farthest known diurnal location was measured by radio telemetry. Roosts shown are: (A) inside home range (bird ID 990), (B) on the edge of the home range (bird ID 951a), and (C) outside the home range (bird ID 894). All roosts were within the Coconino National Forest in northern Arizona during winter 2002–2003.

Bull et al. (1997) reported excavation in ponderosa pine 4–8 years following tree death. We observed Hairy Woodpeckers excavating cavities in snags created by high-severity fire at 2 and 3 years post-wildfire, indicating that high-severity burned ponderosa pine is available for excavation sooner than those created by other means. This is likely because ponderosa pine trees consist of 50–75% sapwood, which typically rots within 2 and appreciably deteriorates by 3 years following wildfire (Kinney 1955, Lowell and Cahill 1996, Bull et al. 1997). Thus, roost trees created by fire are more abundant because patches or swaths of trees die (Schubert 1974) and become available for excavation sooner than unburned snags. While literature exists on the decay process in burned trees (Kinney 1955, Morrison and Raphael 1993, Lowell and Cahill 1996, McHugh and Kolb 2003), little exists for trees succumbing to other mortality agents and how this affects cavity excavation by primary cavity nesters (Jackson and Jackson 2004).

Hairy Woodpeckers used roost trees with on average two times the bark coverage than found for cavity nesters in northeastern Arizona (>40%, Scott 1978). Retention of charred bark likely provides thermoregulatory benefits because temperatures under fire-blackened bark are higher than under non-charred bark (Kinney 1955). This difference could reduce winter energy expenditures of individuals within roosts until retained heat dissipated. Considering that our roost trees were smaller in size than those in other studies (Raphael and White 1984, Horton and Mannan 1988, Saab et al. 2002), intact burned bark on small trees might provide similar insolative values as larger trees with less bark. Alternatively, use of small roost trees with more bark could reflect the abundant availability of small snags created by wildfire and the rarity of large snags (Ganey 1999) in this system.

Hairy Woodpeckers oriented their roosts away from southwest winds that predominate in northern Arizona nightly (Staudenmaier et al. 2002, Acker 2003). Roost cavities were oriented on average 108.4° from southwest, while those that were not were sheltered from winds due to their placement on a northerly slope or within thick unburned vegetation. Non-random orientation of cavity entrances away from prevailing winds was also established for woodpeckers as a group (Conner 1975, 1977; Stauffer and Best 1982) and Downy Woodpeckers using artificial snags (Peterson and Grubb 1983, Petit et al. 1985). Petit et al. (1985) also found cavity entrances oriented more towards prevailing winds were in canyons or on protective slopes. Roost switches may also be a mechanism that decreases roost ventilation and heat loss caused by prevailing winds. We observed three males that changed roosts. The first male in relatively open terrain, maintained a northerly direction after moving, the second changed from a southerly to a northerly direction, and the third moved to a roost tree significantly lower on a north facing slope.

One-quarter to one-third of the roosts we documented were outside the boundaries of the bird's diurnal home range. Thus, diurnal estimates of movement patterns may underestimate the distance birds move in a day as well as home range size based on diurnal home ranges that do not include roosting habitat. Managers concerned with providing habitat requirements for this U.S. Forest Service Management Indicator Species (Ganey 1999) should consider whether diurnal area requirements include or exclude roosts and choose an appropriate home range estimator based on the biology of the birds within their area of charge.

Fire creates snags that could be used as roosts by woodpeckers by either immediately killing the tree, or by damaging it sufficiently that it succumbs to other mortality agents over time. High-severity fire creates high densities of snags quickly, which may become available sooner to woodpeckers, and include a greater range of tree sizes available for use by woodpeckers as roosts. However, these snags have reduced longevity compared with non-fire snags (Raphael et al. 1987, Morrison and Raphael 1993, Hejl 1994). Moderate-severity fire creates snags over a longer time period through secondary mortality agents such as insect attack or drought (Salaman 1934, Flanagan 1996, Santoro et al. 2001, McHugh and Kolb 2003), but susceptibility depends on canopy scorch (McHugh and Kolb 2003). These snags may have greater longevity but are rarer across the landscape (Ganey 1999). Thus, if fire is the predominant mortality agent, or leads to the greatest indirect mortality via secondary mortality agents, suppression inherently decreases snags across the landscape. Reducing all fires to low-severity could remove both sources of snags, as low-intensity ground fires produce little scorch, injury, and resultant mortality and susceptibility to secondary mortality agents (Furniss 1965, Ryan and Reinhardt 1988, Flanagan 1996, Santoro et al. 2001, McHugh and Kolb 2003). It is believed that snags are in low densities (Ganey and Vojta 2004), but it is unknown if northern Arizona forests contain densities of snags that limit roost tree availability. Further study of roost tree availability at the home range and landscape scale, and how natural and prescribed fire affects availability, warrants future examination.

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SPECIES LIMITS IN THE "*SCHISTOCICHLA*" COMPLEX OF *PERCNOSTOLA* ANTBIRDS (PASSERIFORMES: THAMNOPHILIDAE)

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KEVIN J. ZIMMER[3]

ABSTRACT.—The species-group in the genus *Percnostola* that is sometimes placed in the genus "*Schistocichla*" is shown to consist of seven, mostly allopatric, species. All seven are distinct morphologically; when their vocalizations were compared, 19 of 21 pairwise comparisons resulted in differences as great as or greater than those of syntopic species-pairs in this family. Differences in the two remaining comparisons were limited to two vocal characters, but one involved a pair whose ranges appear to abut without apparent physical barriers; members of the second pair were separated geographically by ~2,400 km. Insights into speciation in the complex are relevant to conservation efforts and ultimately will be related to an ongoing genetic study to suggest a phylogeny and contribute to an understanding of avian evolution in Amazonia. *Received 11 October 2005. Accepted 20 July 2006.*

The thamnophilid genus *Percnostola* is currently considered to consist of three species-groups that may not be closely related (Zimmer and Isler 2003). They include (1) a species-pair consisting of *P. rufifrons*, Black-headed Antbird, and *P. arenarum*, Allpahuayo Antbird (Isler et al. 2001); (2) a single species of uncertain affinities: *P. lophotes*, White-lined Antbird; and (3) a group of 12 taxa, sometimes placed in a distinct genus "*Schistocichla*," that are the subject of this paper and which are referred to as the "*Schistocichla* complex."

The *Schistocichla* complex has had a confused taxonomic history since the end of the nineteenth century during which existing and newly described taxa were placed in a number of different genera and lumped or split into two or more species (sequentially: Hellmayr 1906, 1907; Cory and Hellmayr 1924; Todd 1927; Zimmer 1927; Hellmayr 1929; Zimmer 1931; Zimmer and Phelps 1946, 1947). In the process, Todd (1927) created a new genus, *Schistocichla*, for the group, but in his brief diagnosis he did not distinguish *Schistocichla* from the genus *Percnostola* to which the original description of *leucostigma* had been assigned by von Pelzeln (1868). Finally, without explanation, Peters (1951) placed the group in the genus *Percnostola* and assigned the 12 taxa to three species: *P. schistacea* (monotypic), *P. leucostigma* (9 subspecies), and *P. caurensis* (2 subspecies). Peters (1951) decisions were followed by subsequent check-lists (Meyer de Schauensee 1966, 1970; Sibley and Monroe 1990). Ridgely and Tudor (1994) resurrected the genus *Schistocichla* for the complex, which they distinguished from other *Percnostola* species by having rounder and uncrested heads, and spots, not fringing, to their wing coverts. Although we consider it likely that *Schistocichla* ultimately will be restored for the group, we consider this diagnosis inadequate for reasons provided in Braun et al. (2005). We maintain the complex in *Percnostola* pending completion of genetic analysis of species in *Percnostola* and related genera, after which the morphological, vocal, and genetic analyses will be integrated to suggest a phylogeny and an appropriate generic name.

Generic placement of the *Schistocichla* complex is not essential to the present analysis of species limits. The careful definition of species is of vital concern, however, for conservation efforts and is essential for phylogenetic study and reconstruction of the historical processes leading to the distribution of biota in Amazonia. Previously, species and subspecies in the group were defined by the sympatry of

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P. schistacea and *P. leucostigma*, and by morphological characters. To these considerations, this paper adds vocal characters and newly obtained biogeographic knowledge. Vocalizations are valuable indirect measures of gene flow and species limits (Johnson et al. 1999, Helbig et al. 2002, Remsen 2005) for antbirds and other suboscine passerines in which vocalizations are thought not to be learned (Isler et al. 1998, Baptista and Kroodsma 2001). The objective of this paper is to use vocal characters to improve understanding and recognition of species limits in the *Schistocichla* complex.

METHODS

The *Schistocichla* complex of *Percnostola* antbirds (Zimmer and Isler 2003) consists of: *P. leucostigma*, Spot-winged Antbird, which includes nine subspecies (*P. l. subplumbea*, *P. l. obscura*, *P. l. saturata*, *P. l. leucostigma*, *P. l. intensa*, *P. l. brunneiceps*, *P. l. infuscata*, *P. l. humaythae*, and *P. l. rufifacies*); *P. schistacea*, Slate-colored Antbird, considered monotypic; and *P. caurensis*, Caura Antbird, with two subspecies (*P. c. caurensis* and *P. c. australis*). Vocal recordings of *P. l. intensa* and *P. c. caurensis* were unavailable for this study. The remaining 10 taxa are maintained as units of analysis, and we use "*schistacea*," "*caurensis*" and subspecies names of *P. leucostigma* (without initials of genus or species) to reference populations.

The definition of geographic units for the analysis began with published distributional boundaries (Fig. 1A, B). However, because of the possibility that plumage-based subspecies distributions may not fully express the existence of independently evolving populations as may be reflected in their vocalizations, ranges of *P. leucostigma* subspecies were divided further into 30 geographic clusters (Fig. 1C) based on knowledge of the biogeography of other thamnophilid antbirds. For example, if a river was known to define ranges of other closely related pairs of thamnophilid taxa, recordings obtained on opposite sides of that river were separated into clusters. Geographic clustering of *humaythae* recordings also took into consideration that *P. leucostigma* "*major*" Todd (1927) had been described from the region immediately south of the Amazon but synonymized with *humaythae* by Hellmayr (1929). We compared vocal data for adjacent geographic clusters and aggregated clusters in which vocalizations did not differ diagnosably. Thus, *P. leucostigma* clusters were gradually consolidated until the aggregated populations evidenced diagnostic vocal differences. Similarly, the smaller geographic range of *P. schistacea* was divided initially into three clusters to test for geographic variation. Recordings of *P. caurensis* were available from only one location (Zimmer 1999).

Vocal characters used to examine species limits were: (1) number of notes, (2) duration, (3) pace, (4) change of pace, (5) note shape, (6) change in note shape, (7) note length, (8) change in note length, (9) interval length, (10) change in interval length, (11) peak frequency, and (12) change in peak frequency (Appendix 1). Conceptually, these characters were considered independent from one another; variation in one character could occur without resulting in a different outcome for another character. We also recognized the possibility, however, that some characters might be linked, given their likely common ancestry. Consequently, we culled pairs of character measurements that had correlation coefficients ≥0.80.

Tape recordings (391 recordings from 265 localities) were compiled from natural sound archives, from our personal inventories, and from unarchived contributions from other individuals (Appendix 2). We reviewed every recording to identify the number and gender of individuals vocalizing and to label every vocalization as to type. Loudsongs (following Willis 1967) refer to the ringing series of notes delivered in a consistent pattern that is often described simply as song. Canary 1.2 and Raven 1.2 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York, USA) were used to make a spectrogram of every vocalization type delivered by each individual of either gender on every recording. Qualitative characters were obtained by examining printed copies of all clearly delineated spectrograms (i.e., sampling was not used). We considered a qualitative character to be diagnostic when visual examination completely distinguished every spectrogram of one population from another. If there was any uncertainty, we conducted "blind tests." Spectrograms were stripped of

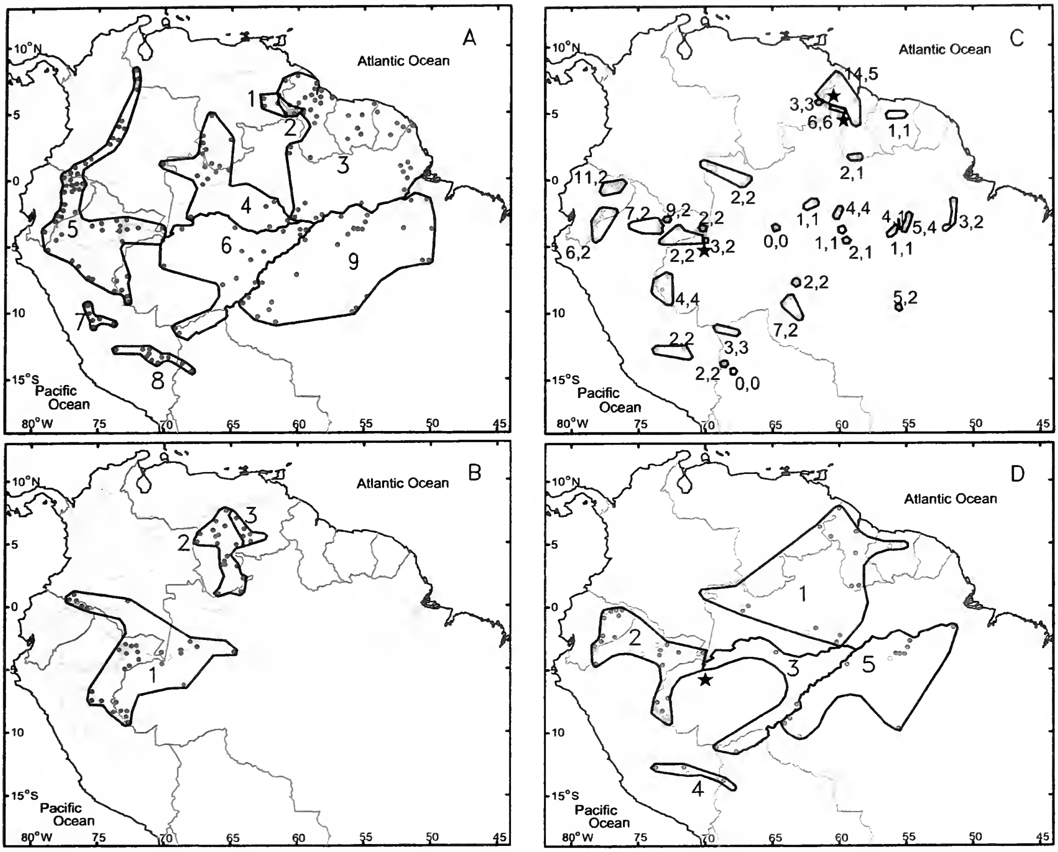

FIG. 1. Geographic ranges and recording locations. Locations are assigned to geographic sectors (Isler 1997). (A) Known geographic ranges of nine taxa considered by Peters (1951) to be subspecies of *Percnostola leucostigma*. 1 = *P. l. obscura*; 2 = *P. l. saturata*. 3 = *P. l. leucostigma*; 4 = *P. l. infuscata*; 5 = *P. l. subplumbea*; 6 = *P. l. humaythae*; 7 = *P. l. intensa*; 8 = *P. l. brunneiceps*; 9 = *P. l. rufifacies*. Solid circles = locations documented by specimens, recordings, photographs, or records by experienced observers. (B) Known geographic ranges of the three remaining taxa in the *Schistocichla* complex. 1 = *Percnostola schistacea*; 2 = *P. caurensis australis*; 3 = *P. c. caurensis*. Symbols as in Fig. 1A. (C) Initial stage locations, number of recordings, and sample sizes of male loudsongs in *P. leucostigma* populations (including *saturata* and *obscura*) analyzed as populations. Solid circles = recording locations of male loudsongs. Open circles = recording locations of other vocal types. Stars = locations where vocally distinct populations were found to be parapatric. Numbers = total number of male loudsong recordings followed by sample size. (D) Final stage locations of recordings of five taxa currently considered subspecies of *P. leucostigma*. Symbols as in (C). Lines encircle recordings ascribed to taxa: 1 = *leucostigma*; 2 = *subplumbea*; 3 = *humaythae*; 4 = *brunneiceps*; 5 = *rufifacies*.

any identification except a randomly selected code number, sorted visually according to perceived differences, and considered to differ diagnosably only if the resultant groups distinguished populations unequivocally.

Calls were used solely as discreet characters (presence/absence in population repertoires and qualitative differences in note shape). Quantitative characters were restricted to a sample of loudsong recordings. Sample sizes reflect number of individuals, not number of vocalizations measured. We measured three vocalizations of each vocalization type for at least six individuals of every population, although it was not possible to achieve this goal because of recording inadequacies. If more than six suitable recordings were available, we sought to distribute the sample throughout the region defined for the population. Quantitative measures were obtained from spectrograms projected on a 43-cm screen from a Macintosh G4 computer using default settings of Canary

1.2 (Charif et al. 1995), except the display was set to smooth, overlap was adjusted from 50 to 93.7% depending on recording quality, and contrast was adjusted according to recording intensity with care taken to retain all elements of the vocalization. These were supplemented by recordings projected on a 43-cm screen by a Dell 8300 computer using parallel settings of Raven 1.2 (Charif et al. 2004). Cursor measurements were typically at scales of 0.12 sec/cm and 1.5 kHz/cm.

Diagnostic differences must be discrete, non-overlapping character states that have the potential for unambiguous signal recognition (Isler et al. 1998, 1999). Ranges of samples of continuous variables could not overlap, and the likelihood that ranges would not overlap with larger sample sizes was estimated by requiring the means ($\bar{x}$) and standard deviations (SD) of the population with the smaller set of measurements (a) and the population with the larger set of measurements (b) to meet the test:

$$\bar{x}_a + t_a SD_a \leq \bar{x}_b - t_b SD_b$$

where t_i = the t-score at the 97.5 percentile of the t distribution for $n - 1$ degrees of freedom. A similar test could not be used for ratios, which are not distributed normally, and a non-parametric bootstrap simulation was used to examine statistical significance. We compared the difference between the means (DBM) for the two taxa being analyzed and the two groups of generated data of the same sample sizes. The method generated 10,000 sample population pairs, with replacement, and compared the DBM between the two compared species to the distribution of DBMs of the simulated populations. The result was distributed normally, and significance assigned according to the rules of this distribution.

We assessed taxonomic status based on vocal distinctions, accepting current subspecies definitions as reflecting diagnostic morphological differences. We recommended species status for populations that differed diagnostically in both vocalizations and morphology. Vocal differences were considered diagnostic at the species level if the analysis revealed three or more diagnostic vocal characters (Isler et al. 1998). This guideline has been recognized as a relevant "yardstick" in considering species status for allopatric thamnophilid populations (Johnson et al. 1999, Helbig et al. 2002, Remsen 2005). Fewer vocal characters were considered acceptable when populations were parapatric without obvious geographic barriers or highly differentiated morphologically. Existing taxa that did not meet vocal requirements for recommendations as distinct species were maintained as subspecies pending results of an ongoing molecular study.

RESULTS

Loudsongs.—Most vocal differences among taxa occurred in their loudsongs (Fig. 2). Males and females gave similarly structured loudsongs, although female loudsongs tended to have fewer notes and to be slower paced. Only loudsongs that could be attributed to males were used in the analysis because too few recordings of loudsongs were clearly identified as being delivered by females.

No vocal differences were found between *obscura* and *saturata* of the Gran Sabana region of southeastern Venezuela and adjacent Guyana (Fig. 1A). Their vocal data were aggregated in this study under the name of *saturata* which has priority. When loudsongs of *saturata* were compared to the remaining taxa in the "*Schistocichla*" complex (Table 1, Appendix 1), they differed diagnostically in at least five vocal characters in each pair-wise comparison with one exception, the *saturata-brunneiceps* comparison. Only two vocal characters, visual differences in "long calls" and patterns of peak frequencies of loudsongs, differed diagnosably between *saturata* and *brunneiceps*. Measurements of three additional loudsong characters (pace, note length, and peak frequency) did not overlap, but our statistical test suggested that overlap was possible with larger samples.

Nominate *leucostigma*, *infuscata*, *subplumbea*, and *humaythae* are distributed around northern and western Amazonia (Fig. 1A). Recordings of *infuscata* were merged into *leucostigma* in the final analysis because we found no diagnostic differences between them. No vocal differences were identified within the range of *humaythae* after dividing recordings north and south of seven degrees South latitude (samples from the south, n = 7, included two recordings from the type locality of *humaythae*; samples from the north,

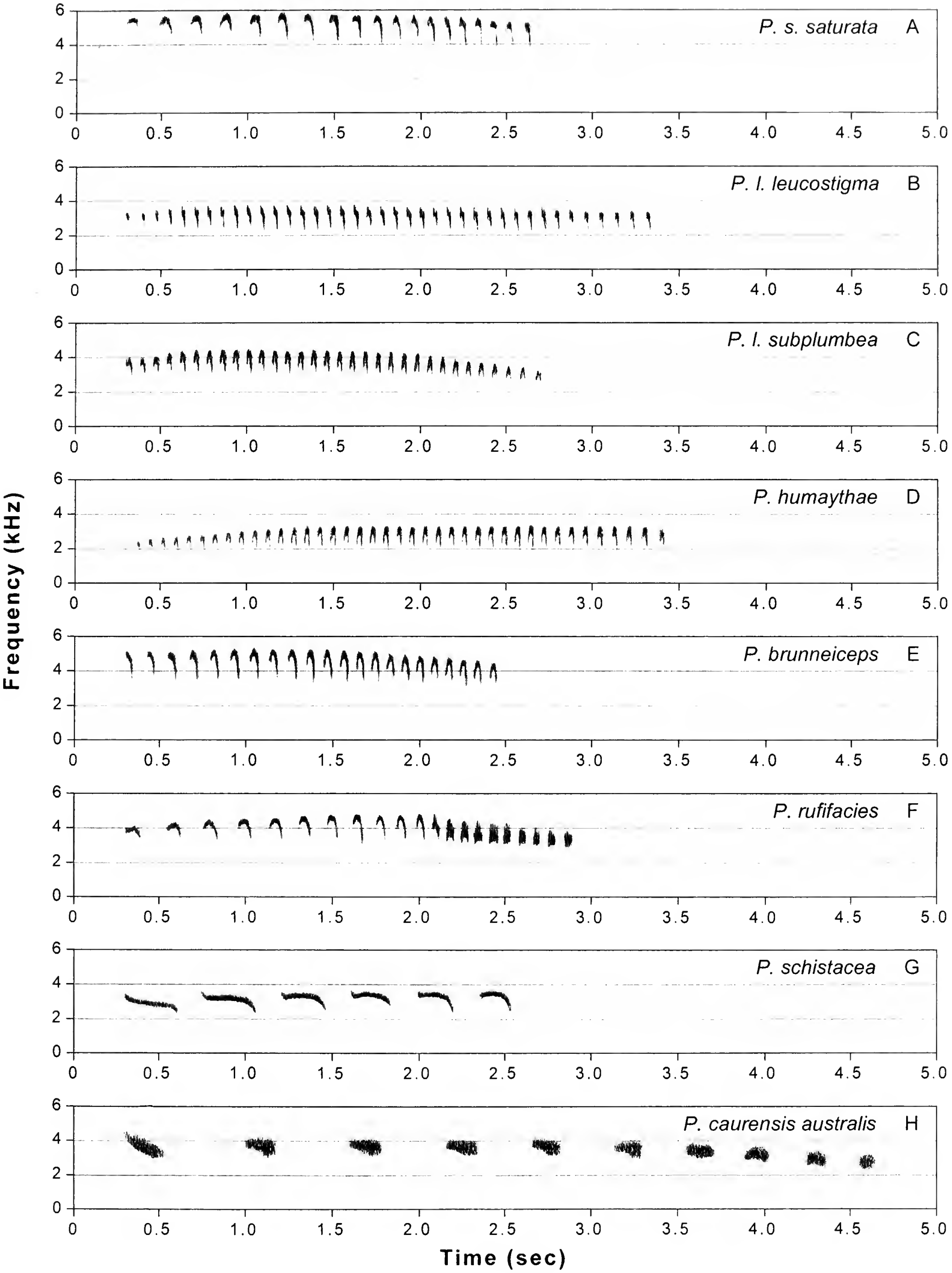

FIG. 2. Loudsongs of taxa in the "*Schistocichla*" complex. Nomenclature follows recommendations of this paper. (A) *P. s. saturata*, Kaieteur Fall, Guyana (ISL-MJB.001:40). (B) *P. l. leucostigma*, Manaus region, Amazonas, Brazil (ML 74353). (C) *P. l. subplumbea*, La Selva Lodge, Napo, Ecuador (ISL-RAB.001:11). (D) *P. humaythae*, Camino Mucden, Pando, Bolivia (ML 38882). (E) *P. brunneiceps*, Amazonia Lodge, Madre de Dios, Peru (ISL-JCA.008.01). (F) *P. rufifacies*, Itapoama, Pará, Brazil (ISL-BMW.101:34). (G) *P. schistacea*, Igarapé Ouro Preto, Acre, Brazil (ISL-BMW.138:18). (H) *P. caurensis australis*, Serranía de Cerbatana, Bolívar, Venezuela (ISL-KJZ.064:12). (Archive acronyms in Appendix 2.)

TABLE 1. Diagnostic vocal characters distinguishing male loudsongs and calls of *Percnostola* taxa for which diagnosable differences were found. Nomenclature follows recommendations of this paper. Recordings were unavailable for *P. l. intensa* and for the nominate form of *P. caurensis*, vocalizations of *P. s. saturata* and *P. s. obscura* were indistinguishable, and vocalizations of *P. l. leucostigma* and *P. l. infuscata* were indistinguishable. Sample sizes reflect number of individuals.

Taxa	*n*	*P. l. leucostigma*	*P. l. subplumbea*	*P. humaythae*	*P. brunneiceps*	*P. rufifacies*	*P. schistacea*	*P. caurensis australis*
P. saturata	16	6	6	6	2	5	9	7
P. l. leucostigma	5		1	1	4	7	7	8
P. l. subplumbea	8			2	4	7	7	7
P. humaythae	16				4	8	8	9
P. brunneiceps	18					4	9	6
P. rufifacies	12						8	6
P. schistacea	6							8
P. caurensis australis	13							

n = 5, included three recordings from the south bank of the Amazon near the type locality of "*major*"). Vocal distinctions among *leucostigma* (including *infuscata*), *subplumbea*, and *humaythae* loudsongs (sample distributions Fig. 1D) were found in peak frequency and the pattern of peak frequency change. Peak frequency levels of *humaythae* loudsongs were lower throughout the first half of the loudsong, as exemplified by the second note (Fig. 3A), diagnostically when compared to *subplumbea*, but not to *leucostigma*. Differing patterns of peak frequency change were apparent visually (Fig. 2). Peak frequencies of *leucostigma* notes were nearly constant (although often rising slightly at the beginning and dropping slightly at the end); those of *subplumbea* increased and decreased in frequency; whereas those of *humaythae* increased initially and then flattened out (although sometimes dropping slightly in the final few notes). These differences were expressed quantitatively (Fig. 3B); the ratio of the peak frequency of the second note divided by that of the penultimate note differed diagnostically between *leucostigma* and *subplumbea* and between *subplumbea* and *humaythae*.

The remaining three subspecies of *P. leucostigma* (*intensa*, *brunneiceps*, and *rufifacies*) are distributed along the base of the Andes in Peru and Bolivia and east of the Rio Madeira in Brazil (Fig. 1A; sample distributions Fig. 1D). Of these, vocalizations of *rufifacies* were most distinct, and a shift in note shape near the midway point of its loudsong was unique (Fig. 2). A mean difference of 6.0 vocal characters distinguished *rufifacies* from other taxa currently considered subspecies of *P. leucostigma* (Table 1). Four vocal characters distinguished loudsongs of *brunneiceps* from all other *leucostigma* subspecies except *saturata* (Table 1); both *brunneiceps* and *saturata* had loudsongs that initially were slowly paced and then accelerated (Fig. 2). Vocal recordings of *intensa* were unavailable.

The final three taxa in the assemblage have been placed in two species, the monotypic *schistacea* and *caurensis* including the subspecies *australis* (Fig. 1B). Loudsongs of *schistacea* were disaggregated into three geographic clusters to investigate the possibility that it was a polytypic species. Loudsongs recorded north of the Amazon tended to be

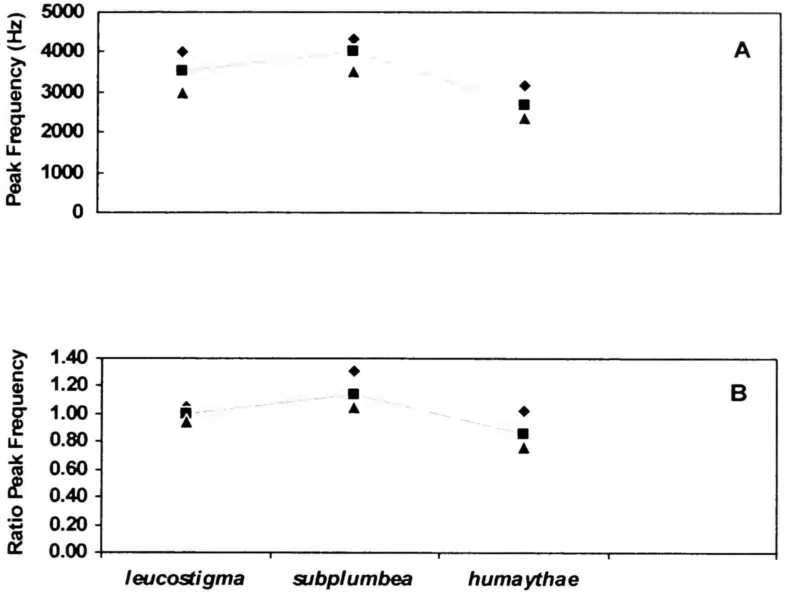

FIG. 3. Selected frequency characteristics of loudsongs of *leucostigma*, *subplumbea*, and *humaythae* arranged geographically from northeast to northwest to southwest (Fig. 1A). Lines connect means. Symbols above and below line reflect maximum (diamond) and minimum (triangle) values. (A) Frequency level as reflected in the peak frequency of the second note in the loudsong. (B) Pattern of frequency change as measured by the ratio of the peak frequency of the second note divided by that of the penultimate note.

slower paced with corresponding longer terminal notes than those recorded immediately south of the river. These differences did not meet our statistical test, and loudsongs from the extreme southern portion of its range (Acre, Brazil) were intermediate. Vocalizations of *schistacea* were aggregated for the final analysis. Vocal data were available for *caurensis* from only one location. Numerous diagnostic differences in loudsong structure between *schistacea* and *caurensis*, and between each and the remaining taxa were apparent in visual examinations (Fig. 2) and quantitative vocal characters (Table 1).

Calls.—Vocal repertoires of all taxa included a "long call," a descending whistle sounding like *teeeeur* (Fig. 4A–C). The figure illustrates the variety of forms of this call, and we identified no diagnostic differences among taxa with two exceptions. The long call of *saturata* (n = 9) was preceded by an abrupt note at a higher pitch (Fig. 4D), and that of *caurensis* (n = 10) was strongly frequency modulated and consistently included an overtone (Fig. 4E). A second principal type was a "short call" consisting of multiple, closely spaced vertical elements and imparting a vibrating quality, sounding like *tchick* (Fig. 4F). It was given by all taxa. The single recording of the short call of *caurensis* appeared to be simpler structurally, but the difference was not considered diagnostic pending acquisition of additional recordings. The third principle type of call consisted of a narrow vertical note repeated in short series of 3–14 notes having the quality of a "rattle" (Fig. 4H). No differences in the rattle were diagnosed among taxa. The long call, short call, and rattle were frequently intermixed and delivered in rapid succession by birds of both gender.

Beyond the three principal types of calls, a "multi-note series" was recorded for some taxa. In *rufifacies*, this was a repetition of the long call (Fig. 4J). In *leucostigma* and *subplumbea*, however, a short series was recorded in which the initial part of the note rises, forming an inverted "U" (Fig. 4K), and a similar call was recorded for *schistacea* (Fig. 4L). A larger sample of recordings may reveal diagnostic differences among taxa in the multi-note series. Finally, *schistacea* was found to have a fifth type in its repertoire, a "chevron

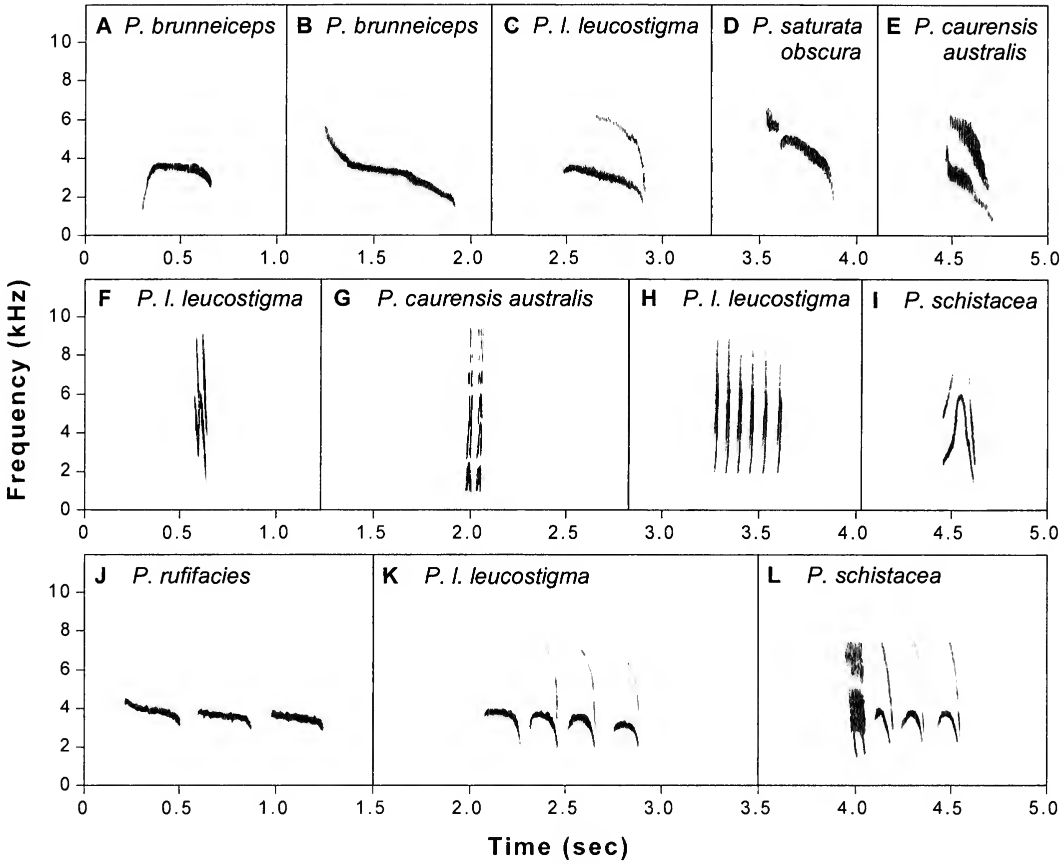

FIG. 4. Calls of taxa in the "*Schistocichla*" complex. Nomenclature follows recommendations of this paper. (A) Long call *P. brunneiceps*, Amazonia Lodge, Madre de Dios, Peru (ISL-BMW.031:13). (B) Long call *P. brunneiceps*, Río Tuichi, La Paz, Bolivia (ISL-BMW.117:31). (C) Long call *P. l leucostigma*, La Escalera, lower elevations, Bolívar, Venezuela (NSA 26680). (D) Long call *P. saturata obscura*, La Escalera, upper elevations, Bolívar, Venezuela (NSA 68312). (E) Long call *P. caurensis australis*, Serranía de Cerbatana, Bolívar, Venezuela (ISL-KJZ.063:27). (F) Short call *P. l. leucostigma*, Manaus region, Amazonas, Brazil (ML 74353). (G) Short call *P. caurensis australis*, Serranía de Cerbatana, Bolívar, Venezuela (ISL-KJZ.063:22). (H) Rattle *P. l. leucostigma*, La Escalera, lower elevations, Bolívar, Venezuela (NSA 26680). (I) Chevron-shaped call *P. schistacea*, Quebrada Sucusari, Loreto, Peru (ML 47797). (J) Multi-note call *P. rufifacies*, Itapoama, Pará, Brazil (ISL-BMW.101:34). (K) Multi-note call *P. l. leucostigma*, Dubulay Ranch, Guyana (ISL-MBR.002.01). (L) Multi-note call *P. schistacea*, P. N. Serra do Divisor, Acre, Brazil (ISL-BMW.128:20).

shaped call," (Fig. 4I) that was unique in the complex.

New Geographic Information.—Recent field studies have documented two cases of apparent parapatry of taxa in the "*Schistocichla*" complex. First, *saturata* and *leucostigma* have been found to be parapatric in Guyana and eastern Venezuela. Second, we tape-recorded two taxa along the right bank of the lower Rio Javari, Amazonas, Brazil. At the Reserva Natural Palmarí (04° 17′ S, 70° 18′ W), loudsongs were typical of *subplumbea*, whereas near the mouth of the Rio Javari in the vicinity of Benjamin Constant (04° 22′ S, 70° 02′ W), loudsongs matched those of *humaythae*. The distance between the two sites is approximately 60 km with no obvious topographic barrier between them, suggesting parapatry or the possibility of sympatry.

DISCUSSION

We propose the following taxonomic positions and English names for members of the complex. The sequence of species is tentative, awaiting genetic analysis.

- *Percnostola saturata* (Salvin)—Roraiman Antbird
  - *P. s. saturata* (Salvin)
  - *P. s. obscura* (Zimmer and Phelps)
- *Percnostola leucostigma* von Pelzeln—Spot-winged Antbird
  - *P. l. leucostigma* von Pelzeln
  - *P. l. infuscata* (Todd)
  - *P. l. subplumbea* (Sclater and Salvin)
  - *P. l. intensa* (Zimmer)
- *Percnostola humaythae* (Hellmayr)—Humaita Antbird
- *Percnostola brunneiceps* (Zimmer)—Brownish-headed Antbird
- *Percnostola rufifacies* (Hellmayr)—Rufous-faced Antbird
- *Percnostola schistacea* (Sclater)—Slate-colored Antbird.
- *Percnostola caurensis* (Hellmayr)—Caura Antbird
  - *P. c. caurensis* (Hellmayr)
  - *P. c. australis* (Zimmer and Phelps)

Our results for *saturata* were consistent with those of Braun et al. (2005) who recommended species status based on morphological and genetic differences as well as a smaller sample of vocalizations than was used in this study. A large number of vocal characters distinguished *saturata* from all taxa except *brunneiceps* (Table 1). Vocal differences between *saturata* and *brunneiceps* came close to meeting our guideline, however. The wide geographic disjunction of their ranges (~2,400 km) suggests that *saturata* and *brunneiceps* have evolved independently and that loudsong similarities are homoplasious. Species status for *brunneiceps* was supported by the finding that it differed from the remaining taxa by an average of five and a minimum of four vocal characters.

The fewest vocal differences were found among *leucostigma*, *subplumbea*, and *humaythae* (Table 1). However, assessment of taxonomic status must also consider geographic relationships. The geographic pattern of values of vocal characters (Fig. 3) is inconsistent with a cline, with values rising between *leucostigma* and *subplumbea* and decreasing sharply between *subplumbea* and *humaythae*. Clinal variation in a vocal character of another thamnophilid antbird was documented to correspond with genetic intergradation (Isler et al. 2005), and the lack of clinality indicated an absence of intergradation. The conclusion that *subplumbea* and *humaythae* were specifically distinct was buttressed by apparent parapatry along the Rio Javari. Vocal differences between *subplumbea* and nominate *leucostigma* were insufficient, however, to raise *subplumbea* to the species level. Also best maintained as subspecies of *leucostigma* are *infuscata*, for which no diagnostic vocal differences with *leucostigma* were identified, and *intensa*, for which no vocal recordings were available. The latter is based on plumage similarities, although future vocal and genetic analyses may reveal that *intensa* is related to *brunneiceps* as both taxa occur in Andean foothills. Our results supported Hellmayr's (1929) conclusion that "*major*" (Todd 1927) is a synonym of *humaythae*.

Large numbers of vocal characters distinguished *rufifacies*, *schistacea*, and *caurensis* which are considered specifically distinct. Of the taxa currently considered subspecies of *P. leucostigma*, *rufifacies* was most dissimilar vocally and differed from the other taxa by an average of 7.9 and a minimum of five vocal characters (Table 1). The two taxa, *schistacea* and *caurensis*, currently accepted as distinct species (Peters 1951, Sibley and Monroe 1990), differed by a minimum of five vocal characters and averages of 10.0 and 9.0, respectively. Analysis of vocal variation within the range of *schistacea* indicated that it was best maintained as a monotypic species.

Two currently named subspecies are dubiously distinct but are maintained pending acquisition of vocal and/or genetic materials. Hilty (2003 and pers. comm.) examined a large series of specimens at the Museo de Phelps and concluded that *P. c. australis* did not differ appreciably from the nominate form and was not worthy of recognition. We also follow Braun et al. (2005) in maintaining *obscura* as a subspecies of *P. saturata* pending genetic analysis.

Future Work.—Further recommendations regarding taxonomic status and estimation of the phylogeny of the *Schistocichla* complex await completion of the genetic study now underway. Vocal analysis of additional recordings would be valuable, especially recordings that permit *P. l. intensa* to be included in the analysis. Comparison of the behavioral context and evolution of vocalizations with those of other thamnophilid groups should be rewarding. For example, the similarity of calls among different populations and species in the *Schistocichla* complex was in stark contrast to the distinctive qualities of calls in the *Hypocnemis cantator* complex, another widespread Amazonian group of antbirds (Isler et al. 2007). A thorough understanding of geographic variation in the *Schistocichla* complex offers a potentially valuable window on avian evolution in the Neotropics but requires additional field work, including the collection of specimens, tissue, behavioral information, and vocal recordings from regions in which these are currently unknown.

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APPENDIX 1

Pairwise comparisons of vocal characters diagnosing male loudsongs and calls of populations in the "*Schistocichla*" complex. Sequence follows Table 1 from left to right and top to bottom. All measured characters refer to loudsongs; differences among calls were diagnosed solely by presence/absence of a type of call and by note shape.

Vocal characters were defined as follows: (1) Number of notes: inclusive of all notes. (2) Duration: time (sec) from beginning of first note to end of ultimate note. (3) Pace: notes/sec, measured from beginning of first note to end of ultimate interval. (4) Change of pace: notes and following intervals were separated into three sections most equivalent in time, pace was computed for each section, and ratios were used to compare sections. Sections are labeled 1, 2, and 3, consecutively, and 1/3, for example, indicates section 1 divided by section 3. (5) Note shape: qualitative, defined in the following paragraph. (6) Change in note shape: qualitative. (7) Note length: lengths in millisec of first, second, middle, penultimate, and ultimate notes, labeled 1 through 5 consecutively. (8) Change in note length: comparisons of note lengths expressed in ratios; 1/5, for example, indicates note 1 divided by note 5. (9) Interval length: lengths in millisec of intervals following first, second, middle, and penultimate notes, labeled 1 through 4 consecutively. (10) Change in interval length: comparisons of interval lengths expressed in ratios; 1/4, for example, indicates interval 1 divided by interval 4. (11) Peak frequency: the highest frequencies attained by first, second, middle, penultimate, and ultimate notes. Numerical labels same as for notes. (12) Change in peak frequency: comparisons of peak frequencies expressed in ratios; numerical labels same as for change in note length.

We used the following terms in describing note shape. "Downslurred" indicates a decrease in note frequency (i.e., the spectrogram trace goes from a higher to a lower frequency). An "upslurred" note goes in the opposite direction. A "flat" note shows little or no change in frequency (a horizontal line on the spectrogram). Frequency gradually increases and decreases in a "rounded" note. A "chevron" resembles an inverted V with a sharp point at the highest frequency. "Frequency-modulated" notes produce a spectrogram trace similar to a "zig-zag" sewing machine stitch within the confines of the general shape of the note. "Clear" notes are represented on a spectrogram by tracings with distinct edges, whereas a note lacking a clear shape is "poorly defined". "Note shape pattern" describes how the shapes of notes change throughout a multi-note vocalization.

Visual identifications of frequency pattern were in reference to a horizontal line drawn through the frequencies of the vocalization. "Peak frequency" refers to the highest frequency attained by the main body of an individual note. "Peak frequency pattern" describes how the highest frequencies of notes change through the course of a multi-note vocalization. "Increase," "flat," and "decrease" refer to changes of peak frequencies among the notes in a series.

saturata versus *leucostigma*.—(1) Change of pace: *leucostigma* accelerates at beginning and decelerates at end; *saturata* accelerates throughout and at a faster rate at beginning as measured in pace ratio of sections 1/2, 1/3, 2/3. (2) Note duration: *leucostigma* notes are shorter initially as measured in length of note 2. (3) Interval duration: *leucostigma* intervals are shorter throughout most of loudsong as measured in length of interval 2. (4) Peak frequency: *leucostigma* lower throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (5) Change in peak frequency: *leucostigma* increases and decreases gradually; *saturata* first half is flat or increases gradually and then decreases sharply as measured in ratio of peak frequencies 2/5. (6) Long Call: note shape differs.

saturata versus *subplumbea*.—(1) Pace: *saturata* is slower as measured in pace sections 1, 2. (2) Change of pace: *saturata* accelerates throughout and at a faster rate at beginning; *subplumbea* accelerates at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Change in note length. *saturata* notes shorten; *subplumbea* lengthen or are nearer to even as measured in ratio of notes 1/4, 1/5. (4) Peak frequency: *saturata* higher throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (5) Change in peak frequency: *saturata* first half is flat or increases slightly; *subplumbea* first half increases more obviously as measured in ratio of peak frequencies 2/3. (6) Long Call: note shape differs.

saturata versus *humaythae*.—(1) Pace: *saturata* is slower as measured in pace sections 1, 2, 3. (2) Change of pace: *saturata* accelerates throughout and at a faster rate at beginning; *humaythae* accelerates at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Change in note duration: *saturata* notes shorten or are close to even; *humaythae* notes lengthen in first half of loudsong as measured in ratio of notes 2/3, 2/4. (4) Peak frequency: *saturata* higher throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (5) Change in peak frequency: *saturata* initially flat or increases slightly, then decreases sharply; *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5. (6) Long Call: note shape differs.

saturata versus *brunneiceps*.—(1) Change in peak frequency: distinguished by the slower pace of *saturata* (no overlap with *brunneiceps* but statistically not significant given current samples) combined with the steeper decrease in frequency in the final third. (2) Long Call: note shape differs.

saturata versus *rufifacies*.—(1) Note shape: although notes of both are more or less chevron-shaped, notes of *rufifacies* are clearly downslurred throughout first half of songs whereas those of *saturata* only occasionally lack upslur in first few notes. (2) Change in note shape: *saturata* notes maintain clear shape; *rufifacies* become frequency modulated. (3) Peak frequency: *saturata* higher throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (4) Change in peak frequency: *saturata* final notes decrease gradually although somewhat sharply; *rufifacies* final notes decrease abruptly and sharply. (5) Long Call: note shape differs.

saturata versus *schistacea*.—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Note shape: *schistacea* notes are flat or slightly rounded; *saturata* notes are chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *saturata* notes maintain shape although initial notes sometimes lack upslur side of chevron. (4) Interval duration: *schistacea* interval 4 longer. (5) Change in interval duration: *schistacea* intervals near even in length; *saturata* intervals shorten more as measured by ratios of intervals 1/3, 1/4, 2/4. (6) Peak frequency: *schistacea* notes 1, 2, 3, and 4 lower. (7) Change in peak frequency: in second half of loudsong *schistacea* notes increase gradually or are flat; second half notes of *saturata* notes decrease to a level lower than initial notes as measured by ratios of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (8) Long call: Note shape differs. (9) Chevron-shaped call: found only in *schistacea*.

saturata versus *caurensis*.—(1) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *saturata* notes are chevron shaped. (2) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *saturata* notes maintain shape although initial notes sometimes lack upslur side of chevron. (3) Note duration: *caurensis* notes are longer throughout as measured in length of notes 1, 2, 3, 4, 5. (4) Interval duration: *caurensis* intervals are longer throughout most of loudsong as measured in length of intervals 1, 2. (5) Peak frequency: *caurensis* lower throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (6) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *saturata* initially flat or increases slightly, then decreases sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (7) Long Call: note shape differs.

leucostigma versus *subplumbea*.—(1) Change in peak frequency: *leucostigma* loudsongs are mostly flat, increasing and decreasing slightly; *subplumbea* loudsongs decrease sharply in the final quarter as measured in ratio of peak frequencies 2/4, 3/4.

leucostigma versus *humaythae*.—(1) Change in peak frequency: *leucostigma* increases and decreases gradually; *humaythae* increases sharply in first quarter of song, then is flat although terminal few notes may decrease slightly as measured in ratio of peak frequencies 1/3, 2/3.

leucostigma versus *brunneiceps*.—(1) Change of pace: *leucostigma* accelerates at beginning and decelerates at end; *brunneiceps* accelerates throughout as measured in pace ratio sections 1/3, 2/3. (2) Change in interval duration: *leucostigma* near even spacing; *brunneiceps* shortens as measured in ratio of intervals 1/4. (3) Peak frequency: *leucostigma* lower throughout much of loudsong as measured in peak frequency of notes 1, 2, 3. (4) Change in peak frequency: *leucostigma* increases and decreases gradually; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/5.

leucostigma versus *rufifacies*.—(1) Change of pace: *leucostigma* accelerates at beginning and decelerates at end; *rufifacies* accelerates throughout and at a faster rate at beginning as measured in pace ratio of sections 1/2, 1/3, 2/3. (2) Note shape: although notes of both are more or less chevron-shaped, notes of *rufifacies* are more strongly downslurred throughout first half of the vocalization. (3) Change in note shape: *leucostigma* notes maintain clear shape; *rufifacies* become frequency modulated. (4) Note duration: *leucostigma* notes are shorter initially as measured in length of note 2. (5) Change in note duration: *leucostigma* notes lengthen or are close to even; *rufifacies* notes shorten as measured in ratio of notes 2/3. (6) Interval duration: *leucostigma* intervals are shorter throughout most of loudsong as measured in length of intervals 1, 2, 3. (7) Change in peak frequency: *leucostigma* increases and decreases gradually; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply.

leucostigma versus *schistacea*.—(1) Change of pace: *schistacea* accelerates throughout; *leucostigma* accelerates and decelerates as measured by pace ratio of sections 2/3. (2) Note shape: *schistacea* notes are flat or slightly rounded; *leucostigma* notes are either partially or entirely chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *leucostigma* notes maintain shape although initial notes sometimes lack upslur side of chevron. (4) Note duration: *schistacea* notes 1, 2, 3, 4, 5 are longer. (5) Interval duration: *schistacea* intervals 1, 2 are longer. (6) Change in peak frequency: *schistacea* notes increase gradually or are flat in second half of loudsong; corresponding *leucostigma* notes decrease as measured by ratio of peak frequencies 3/5. (7) Chevron-shaped call: found only in *schistacea*.

leucostigma versus *caurensis*.—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Change of pace: *caurensis* accelerates throughout; *leucostigma* accelerates at a slower rate at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3. (3) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *leucostigma* notes are either partially or entirely chevron shaped. (4) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *leucostigma* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in interval duration: *caurensis* shortens; *leucostigma* near even spacing as measured in ratio of intervals 1/4, 2/4. (7) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *leucostigma* increases and decreases gradually as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (8) Long Call: note shape differs.

subplumbea versus *humaythae*.—(1) Peak frequency: *subplumbea* higher through first half of loudsong as measured in peak frequency of notes 1, 2, and 3. (2) Change in peak frequency: *subplumbea* increases and decreases gradually; *humaythae* increases sharply in first quarter of song, then is flat although final 1–3 notes may decrease slightly as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/5.

subplumbea versus *brunneiceps*.—(1) Pace: Pace of *subplumbea* faster at beginning as measured in pace of section 1. (2) Change of pace: *subplumbea* accelerates at beginning and decelerates at end; *brunneiceps* accelerates throughout as measured in pace ratio of sections 1/3, 2/3. (3) Peak frequency: *subplumbea* lower through much of loudsong as measured in peak frequency of notes 1, 2. (4) Change in peak frequency: *subplumbea* increases and decreases gradually; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/3, 2/3.

subplumbea versus *rufifacies*.—(1) Pace: Overall pace: *subplumbea* is faster. (2) Change of pace: *subplumbea* accelerates at beginning and decelerates at end; *rufifacies* accelerates throughout as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Note shape: Although notes of both are more or less chevron-shaped, notes of *rufifacies* are clearly downslurred throughout first half of songs whereas those of *subplumbea* only occasionally lack upslur in first few notes. (4) Change in note shape: *subplumbea* notes maintain clear shape; *rufifacies* become frequency modulated. (5) Note duration: *subplumbea* notes are shorter initially as measured in length of note 2. (6) Change in note duration: *subplumbea* lengthen or are close to even; *rufifacies* notes shorten as measured in ratio of notes 2/4. (7) Change in peak frequency: *subplumbea* increases and decreases gradually; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply.

subplumbea versus *schistacea*.—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Note shape: *schistacea* notes are flat or slightly rounded; *subplumbea* notes are chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *subplumbea* notes maintain shape although initial notes sometimes lack upslur side of chevron. (4) Change in note length: *schistacea* notes shorten; *subplumbea* lengthen or are nearer to even as measured in ratios of notes 1/4, 1/5. (5) Interval length: *schistacea* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in peak frequency: *schistacea* notes increase gradually or are flat in second half of loudsong; second half notes of *subplumbea* notes decrease to a level lower than initial notes as measured in ratios of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5, 4/5. (7) Chevron-shaped call: found only in *schistacea*.

subplumbea versus *caurensis*.—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Change of pace: *caurensis* accelerates throughout; *subplumbea* accelerates at a slower rate at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3. (3) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *subplumbea* notes are chevron shaped. (4) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *subplumbea* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *subplumbea* increases and decreases gradually as measured in ratio of peak frequencies 1/3, 2/3, 3/5. (7) Long Call: note shape differs.

humaythae versus *brunneiceps*.—(1) Pace: pace of *humaythae* faster at beginning as measured in pace of section 1. (2) Change of pace: *humaythae* accelerates at beginning and decelerates at end; *brunneiceps* accelerates throughout as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Note frequency: *humaythae* lower through much of loudsong as measured in peak frequency of notes 1, 2, 3. (4) Change in peak frequency: *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5, 3/4, 3/5.

humaythae versus *rufifacies*.—(1) Change of pace: *humaythae* accelerates at beginning and decelerates at end; *rufifacies* accelerates throughout as measured in pace ratio of sections 1/2, 1/3, 2/3. (2) Note shape: Although notes of both are more or less chevron-shaped, notes of *rufifacies* are clearly downslurred throughout first half of songs whereas those of *humaythae* only occasionally lack upslur in first few notes. (3) Change in note shape: *humaythae* notes maintain clear shape; *rufifacies* become frequency modulated. (4) Note duration: *humaythae* notes are shorter as measured in length of notes 2, 4, 5. (5) Change in note duration: *humaythae* notes lengthen; *rufifacies* notes shorten as measured in ratio of notes 2/3. (6) Interval duration: *humaythae* intervals are shorter throughout most of loudsong as measured in length intervals 1, 2, 3. (7) Peak frequency: *humaythae* lower through much of loudsong as measured in peak frequency of notes 1, 2. (8) Change in peak frequency: *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5, 3/4.

humaythae versus *schistacea*.—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Change of pace: *schistacea* accelerates throughout; *humaythae* accelerates and decelerates, but pace at end slower than beginning as measured in pace ratio of sections 1/3. (3) Note shape: *schistacea* notes are flat or slightly rounded; *humaythae* notes are chevron shaped. (4) Change in note shape: *schistacea* notes become more rounded and downslurred; *humaythae* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Change in note duration: *schistacea* notes shorten or are close to even; *humaythae* notes lengthen in first half of loudsong as measured in ratio of notes 2/3. (6) Interval duration: *schistacea* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (7) Change in peak frequency: *schistacea* increases very gradually throughout or initially increases and becomes flat; *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease as measured in ratios of peak frequencies 2/3, 4/5. (8) Chevron-shaped Call: found only in *schistacea*.

humaythae versus *caurensis*.—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Change of pace: *caurensis* accelerates throughout; *humaythae* accelerates at a slower rate at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3. (3) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *humaythae* notes are chevron shaped. (4) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *humaythae* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in interval duration: *caurensis* shortens; *humaythae* near even spacing as measured in ratio of intervals 1/4, 2/4. (7) Peak frequency: *caurensis* initially higher as measured in peak frequency of note 2. (8) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5, 3/4, 3/5. (9) Long Call: note shape differs.

brunneiceps versus *rufifacies*.—(1) Change of pace: both accelerate throughout, but *rufifacies* accelerates at a faster rate towards end as measured in pace ratio of sections 2/3. (2)

Change in note shape: *brunneiceps* notes maintain clear shape; *rufifacies* become frequency modulated. (3) Peak frequency: *brunneiceps* higher through much of loudsong as measured in peak frequency of notes 1, 2, 3. (4) Change in peak frequency: *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies of 2/3.

brunneiceps versus *schistacea.*—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Note shape: *schistacea* notes are flat or slightly rounded; *brunneiceps* notes are more or less chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *brunneiceps* notes are mostly downslurred in initial half, but then shaped like chevrons. (4) Change in note duration: *schistacea* notes shorten throughout; *rufifacies* notes shorten initially, but are of even length toward end as measured in ratios of notes 4/5. (5) Interval duration: *schistacea* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in interval duration: *schistacea* intervals are near even in length; *brunneiceps* intervals shorten as measured in ratio of intervals 1/3, 1/4, 2/3, 2/4. (7) Note frequency: *schistacea* lower throughout most of loudsong as measured in peak frequency of notes 1, 2, 3. (8) Change in peak frequency: *schistacea* increases gradually throughout or initially increases and becomes flat; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5, 4/5. (9) Chevron-shaped Call: found only in *schistacea.*

brunneiceps versus *caurensis.*—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *brunneiceps* notes are more or less chevron shaped. (3) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *brunneiceps* notes are mostly downslurred in initial half, but then shaped like chevrons. (4) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (5) Peak frequency: *caurensis* lower throughout most of loudsong as measured in peak frequency of notes 2, 3, 4. (6) Long Call: note shape differs.

rufifacies versus *schistacea.*—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Change of pace: *schistacea* accelerates throughout; *rufifacies* also accelerates throughout but pace at end much faster than beginning as measured in pace ratio of sections 1/3. (3) Note shape: *schistacea* notes are flat or slightly rounded; *rufifacies* notes are more or less chevron shaped. (4) Change in note shape: *schistacea* notes become more rounded and downslurred; *rufifacies* notes are mostly downslurred in initial half, but then shaped like chevrons and becoming frequency modulated. (5) Interval duration: *schistacea* intervals are longer in second half; as measured in length of intervals 3, 4. (6) Change in interval duration: *schistacea* intervals near even in length; *brunneiceps* intervals shorten more as measured in ratio of interval 2/3. (7) Change in peak frequency: *schistacea* increases gradually throughout or initially increases and becomes flat; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (8) Chevron-shaped Call: found only in *schistacea.*

rufifacies versus *caurensis.*—(1) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *rufifacies* notes are more or less chevron shaped. (2) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *rufifacies* notes are mostly downslurred in initial half, but then shaped like chevrons and becoming frequency modulated. (3) Note duration: *caurensis* notes are longer throughout as measured in length of notes 1, 2, 3, 4, 5. (4) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2. (5) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies 1/3, 1/5, 2/3, 2/5. (6) Long Call: note shape differs.

schistacea versus *caurensis.*—(1) Note shape: *schistacea* notes are flat or slightly rounded; *caurensis* notes are heavily frequency modulated and poorly defined. (2) Change in note shape: *schistacea* notes become more rounded and downslurred but maintain a clear shape; *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless. (3) Note duration: *schistacea* notes 1, 2, 3 are longer. (4) Interval duration: *schistacea* intervals 1, 2 are shorter. (5) Change in interval duration: *schistacea* intervals remain near even in length; *caurensis* intervals shorten more as measured by ratios of intervals 1/3, 1/4, 2/3, 2/4. (6) Change in peak frequency: *schistacea* increases gradually throughout or initially increases and becomes flat; *caurensis* first half is flat or decreases gradually and then decreases sharply as measured by ratios of maximum frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (7) Long Call: note shape differs. (8) Chevron-shaped Call: found only in *schistacea*.

APPENDIX 2

Recordings Examined.—The following list identifies recordings used in the study by taxon, country, state or department, recording location, and recordist. Numbers following the recordist name identify the number of cuts per recordist per location. Acronyms for recording archives: ML = Macaulay Library, Cornell Laboratory of Ornithology, Ithaca; NSA = National Sound Archive, The British Library, London. ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by Morton and Phyllis Isler. Many of these unarchived recordings either are in the process of being archived or will eventually be archived by the recordists. Nomenclature reflects recommended taxonomic position.

Percnostola s. saturata: (8 recordings; 2 localities). Guyana: Kaieteur Fall (Braun 2 ISL), Mount Roraima (Braun 2 ISL, Milensky 2 ISL, Robbins 2 ISL).

P. s. obscura: (16 recordings; 1 locality). Venezuela: Bolívar; La Escalera (Ascanio 1 ISL, Behrstock 1 ISL, Gullick 2 NSA, Whittaker 3 ISL, Zimmer 9 ISL).

Percnostola l. leucostigma: (57 recordings; 17 localities). Brazil: Amazonas; Manaus, 40–90 km N of (Bierregaard 2 ML, Cohn-Haft 3 ML, Stouffer 1 ML, Whittaker 4 ISL). Guyana: Acarai Mountains (Robbins 2 ISL), Baramita (Robbins 3 ISL), Bartica (Finch 2 ISL), Corona Falls (Finch 1 ML), Dubulay Ranch (Robbins 2 ISL), Iwokrama Forest Reserve (Robbins 3 ISL, Whitney 2 ISL), Kaieteur Fall (Finch 1 ML, Milensky 2 ISL), Onoro River (Braun 2 ISL), Sipu River (Braun 4 ISL), Waruma River (Robbins 5 ISL). Suriname: Brownsberg Nature Reserve (Whitney 1 ISL), Kabalebo Nature Reserve (Whitney 1 ISL), Location unknown (Donahue 1 NSA), Raleigh Vallen (Whitney 1 ISL). Venezuela: Bolívar; El Dorado-La Escalera Road (Ascanio 1 ISL, Macaulay 1 ML, Whitney 1 ISL), La Escalera (Ascanio 1 ISL, Behrstock 1 ISL, Gadd 1 NSA, Gibbs 1 NSA, Innis 1 NSA, D. Willis 3 NSA, Zimmer 3 ISL).

P. l. infuscata: (18 recordings; 4 localities). Brazil: Amazonas; Jaú, P. N. de (Cohn-Haft 2 ISL, K. Rosenberg 1 ISL, Pacheco 1 ISL, Whittaker 1 ISL), São Gabriel da Cachoeira (Whittaker 5 ISL, Zimmer 3 ISL), São Gabriel da Cachoeira, across river from (Whitney 2 ISL, Whittaker 1 ISL, Zimmer 1 ISL). Colombia: Vaupés; Mitú (Hilty 1 ISL).

P. l. subplumbea: (110 recordings; 37 localities). Brazil: Acre; Amônea, Rio (Whitney 1 ISL, presumably this taxon), Boca de Tejo (Whittaker 1 ISL, presumably this taxon), Branco, Rio (Whitney 1 ISL), Minas Gerais 2 (Whitney 1 ISL, presumably this taxon), Serra do Divisor, P. N. (Whitney 4 ISL); Amazonas; Cruzeiro do Sul/Santa Barbara Road (Whitney 1 ISL), Palmarí, R. N. (Whitney 9 ISL, Zimmer 8 ISL). Colombia: Amazonas; Amacayacú, P. N. (Whitney 3 ISL, Willis 1 NSA, tentatively assigned to this taxon). Ecuador: No location (Wall 1 ML); Morona-Santiago; Miazal (Whitney 2 ISL), Santiago, Río (Robbins 1 ML), Taisha (Robbins 1 ML); Napo; Coca (Macaulay 1 ML, Robbins 1 ML), Jatun Sacha (Lewis 2 NSA), La Selva Lodge (Behrstock 2 ISL, G Rosenberg 4 ISL), Limoncocha (Coffey 1 ISL), Loreto, 15–60 km west (Whitney 5 ISL), Maxus Road (Krabbe 5 ISL), Sacha Lodge (Behrstock 1 ISL, Fisher 1 MSA), Suno, Río (Whitney 1 ISL), Tiputini Station (Arvin 4 ISL, Zimmer 3 ISL); Pastaza; Kapawi Lodge (Krabbe 1 ISL). Peru: Amazonas; Huampami (Parker 1 ML); Loreto; Buenavista, Quebrada (Lane 1 ISL), Corrientes, Río (Alvarez 2 ISL), Explorama Lodge (Whitney 2 ISL), Iquitos (Donahue 1 ML), Jeberos (Lane 1 ISL), Libertad (G. Rosenberg 1

ISL), Morona, Río (Lane 1 ISL), Pichana (Whittaker 1 ISL), Sucusari, Quebrada (M. Isler 2 ML, P. Isler 7 ML, Michael 1 ISL, Parker 5 ML, G. Rosenberg 2 ISL, Whitney 2 ISL), Tahuayo Lodge (Hornbuckle 2 ISL), Varillal (Whitney 1 ISL, Whittaker 1 ISL), Yanamono (Donahue 1 ML, Whitney 3 ISL), Yarapa Reserve (Michael 1 ISL); San Martín; Shapaja Road (Lane 2 ISL); Ucayali; Abujao (Meyer 2 ISL).

P. l. intensa: (0 recordings).

Percnostola humaythae: (20 recordings; 10 localities). Bolivia: Pando; Camino Mucden (Parker 2 ML), Chive (Rocha 1 ISL). Brazil: Acre; Humaitá Reserve (Whitney 1 ISL); Amazonas; Amazon Lodge (Zimmer 1 ISL), Benjamin Constant (Whitney 4 ISL), Humaitá (Whitney 2 ISL), Ipixuna, Rio (Whitney 1 ISL), Lábrea (Whitney 1 ISL), Tefé (Coopmans 1 ML), Vila Democracia (Whitney 4 ISL).

Percnostola brunneiceps: (16 recordings; 6 localities). Peru: Cuzco; Consuelo (O'Shea 1 ISL), Quimbiri (Widdowson 1 ISL), Pilcopata (Whitney 1 ISL); Madre de Dios; Amazonia Lodge (Arvin 1 ISL, Innes 1 ISL, Lloyd 1 ISL, R. & V. Yavar 1 ISL, Walker 1 ISL, Whitney 2 ISL). Bolivia: La Paz; Alto Madidi (Hennessey, 3 ISL), Tuichi, Río (Whitney 3 ISL).

Percnostola rufifacies: (58 recordings; 20 localities). Brazil: Amazonas; Atininga, Rio (Whitney 1 ISL), Ipixuna, Rio (Whitney 1 ISL), Mapía, Rio (Zimmer 2 ISL), Paxurizal (Whitney 1 ISL), Pousada Rio Roosevelt, left bank (Whittaker 3 ISL), Sucunduri (Whitney 1 ISL); Mato Grosso; Cristalino, Rio (Whitney 4 ISL; Zimmer 2 ISL); Pará; Altamira, right bank 15 km S (Whitney 1 ISL), Apaçy (Whitney 2 ISL), Aveiro (Whitney 3 ISL), Aveiro, islands between Apaçy and Aviero (Whitney 4 ISL), Carajas, Serra dos (Zimmer 1 ISL), Caxiuanã (Whitney 8 ISL; Whittaker 5 ISL; Zimmer 2 ISL), Itapoama (Whitney 3 ISL), Santarém (Whittaker 3 ISL), Vila Braga (Whitney 1 ISL); Rondônia; Caracol, Rio (Whitney 2 ISL), Pardo, Rio (Zimmer 1 ISL), Porto Velho (Whitney 2 ISL), Rancho Grande, Fazenda (Whittaker 2 ISL; Zimmer 3 ISL).

Percnostola schistacea: (65 recordings, 17 localities). Brazil: Acre; Boca de Tejo (Whittaker 3 ISL), Igarapé Ouro Preto (Whitney 5 ISL), P. N. da Serra do Divisor (Whitney 5 ISL), Riozinho das Minas (Whitney 3 ISL); Amazonas; Barro Vermelha (Whittaker 1 ISL), Benjamin Constant (Whitney 5 ISL), R. N. Palmarí (Whitney 2 ISL, Zimmer 1 ISL). Colombia: Amazonas; P. N. Amaca-yacú (Whitney 4 ISL). Ecuador: Sucumbios; Cuyubeno (J. Rowlett 1 ISL, Whitney 1 ISL). Peru: Loreto; Colonia Angamos (Lane 1 ISL), Pichana (Zimmer 1 ISL), Quebrada Orán (Whitney 4 ISL), Quebrada Sucusari (Budney/Parker 2 ML, Parker 3 ML, P. Isler 1 ML, Whitney 12 ISL), Santa Cecilia (Robbins 1 ML), Yanamono (Whitney 2 ISL); Ucayali; Abujao (Meyer 1 ISL, O'Neill 1 ISL), Cerro Tahuayo (Meyer 5 ISL).

Percnostola caurensis caurensis: (0 recordings).

Percnostola c. australis: (23 recordings; 1 locality). Venezuela: Bolívar; Cerbatana, Serranía de (Zimmer 23 ISL).

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NESTING BIOLOGY OF THE BLACK-BELLIED WREN (*THRYOTHORUS FASCIATOVENTRIS*) IN CENTRAL PANAMA

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ABSTRACT.—We describe the nest and nest site, and provide the first description of the eggs and nesting behavior of the Black-bellied Wren (*Thryothorus fasciatoventris*) in central Panama. Nine nests were found near tree-fall gaps, swamps, and roads in moist tropical forests. Nests were dome-shaped with a circular side entrance. They were composed chiefly of strips of dead palm fronds, and were generally built in places where leaf litter and other debris had accumulated at the convergence of several vines near the forest floor. Both males and females participated in building the nest. Clutch size was three, and eggs were laid on consecutive days. Egg color varied from creamy to beige with faint to dark brown speckles that were more concentrated at the blunt end. Females were the sole incubators, but males fed the incubating females. Only the female brooded the nestlings once they hatched, but both parents fed the nestlings. *Received 20 January 2006. Accepted 31 August 2006.*

Wrens (Troglodytidae) are a species-rich family of small passerines whose greatest diversity is in the New World tropics (Skutch 1960). The Black-bellied Wren (*Thryothorus fasciatoventris*; nominate *Pheugopedius fasciatoventris*, Mann et al. 2006) occurs from central Costa Rica south to western Colombia (Stiles and Skutch 1989). The Black-bellied Wren is common in dense undergrowth thickets and woody vine tangles along forest and woodland edges, and in gaps (Ridgely and Gwynne 1989; Stiles and Skutch 1989; DML, unpubl. data). However, little is known about its breeding biology and nesting behavior. An early note described a nest in thick second growth habitat in Colombia as bulky (Hilty 1977). A second report described the nest in Costa Rica as a globular structure, composed entirely of strips of dead *Heliconia* leaves, with a side entrance sheltered by a visor, 1–2 m above ground level in *Heliconia* thickets, typically on the intersection of several leaf petioles (Stiles and Skutch 1989). Eggs, clutch size, and nesting behavior have not been described. We use data from central Panama to supplement previous descriptions of the nest and nest site, and provide the first description of the eggs, clutch size, and nesting behavior of the Black-bellied Wren.

METHODS

We observed nine nests between May and July in 2001, 2002, and 2004 in moist tropical forest areas in and around Soberania National Park, Republic of Panama (9° 9′ 35″ N, 79° 44′ 36″ W). Six nests were in second growth habitat near the town of Gamboa in the woodland tract known as Gamboa Woods (detailed in Robinson et al. 2000b). Three nests were deep in the forest interior of Soberania National Park on the Limbo study site (described in Robinson et al. 2000a, 2000b). Most nests were monitored approximately every 1–3 days after they were located, but some were monitored only during the building stage, incubation, and/or the nestling stage. Nests were assumed to be depredated if eggs or young nestlings disappeared. We collected information on nest material, measurements, and site characteristics after nests were no longer active. Information on nest material and height was not available for some nests as they were being used for a separate ongoing study of vocal communication in this species (e.g., Logue 2004). Nest height, calculated as the distance from the ground to the bottom of the nest base, was measured with a meter stick (±1 mm). We measured nest and egg dimensions with digital calipers (±0.01 mm). Egg mass was measured with an Acculab Pocket-pro scale (±0.001 g) within two days of clutch

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completion to minimize mass differences due to water loss in the egg.

We recorded parental behavior of both males and females during building, incubation, and nestling stages by direct observation, tracking movements via radio-marked individuals, and video monitoring. Males and females were distinguished by song or by unique combinations of colored leg bands used as part of an ongoing study of vocal communication in this species (11 of the 18 parents were marked; Logue 2004). We observed behavior at different stages of construction during the building stage. We filmed incubation behavior at one nest for 6.7 hrs the day after the last egg was laid. The camera was placed on the ground ~3 m from the nest and concealed with leaf litter. The recorded behavior was transcribed later. We outfitted pairs from two other nests with 0.72-g radios (model BD-2, Holohil Systems Ltd., Carp, ON, Canada; Rappole and Tipton 1991). We tracked movements of radio-marked pairs for 2–3 hrs per day in the early morning for 3–4 days during the incubation period. Time at and away from the nest was recorded for both males and females, but dense vegetation prevented us from identifying whether the bird at the nest was actually incubating or perched next to the nest. We observed parental behavior at two nests during the nestling stage.

RESULTS

Nest 1 was in Gamboa Woods, nests 2–6 were in second growth habitat near the town of Gamboa, and nests 7–9 were deep in the forest interior of Soberania National Park. Five nests were located during the building stage, two during incubation, and two during the nestling stage (Table 1). Each nest was built by a different pair.

Nest Site and Construction.—Nest sites varied in nest patch and microhabitat. Nests 1–6 were within 5 m of roads, nest 8 was within 5 m of a large tree fall gap, and nests 7 and 9 were near edges of swamps. Nest 1 was in a tangle of sharp, mostly dead sedges (Cyperaceae). Nest 6 rested on top of natural debris in a patch of wild sugarcane (*Saccharum spontaneum*). The remaining seven nests were in sites where leaf litter and other debris had accumulated at the convergence of several vines suspended a short distance above the forest floor. Mean nest height was 21.4 cm (±8.8 SD; nests 2–4 and 7–8).

TABLE 1. Date found, stage found, and clutch initiation date for Black-bellied Wren nests in central Panama.

Nest	Date found	Stage	Clutch initiation date
1	15 Jun 2001	Building	21 Jun 2001
2	6 Jul 2002	Building	9–10 Jul 2002
3	6 Jul 2002	Nestling	—
4	27 Jun 2002	Building	3 Jul 2002
5	19 Jul 2004	Incubation	—
6	28 Apr 2003	Incubation	—
7	10 May 2004	Building	17 May 2004
8	13 Jun 2004	Building	16 Jun 2004
9	3 Jul 2004	Nestling	—

All nests were dome-shaped and had a circular side entrance shielded by a small visor (<20 mm in depth). Nest exteriors appeared disheveled, with fibers oriented in many directions and projecting loose ends. The nest interior was a spherical chamber with a well-defined nest cup and roof. Nests in the forest interior were exclusively of dead plant material. Most of this consisted of frond strips and leafstalk fibers of understory palms (Palmae) with some leaves and small rootlets from a variety of tree species (Fig. 1). Interior chambers were lined with a thin layer of partially decomposed dicotyledon leaves. Nests in second growth habitat were similar in structure but differed in types of material used; nests were composed primarily of dead *Saccharum* leaves and strips of dead palm fronds. The inside chambers of these nests were lined with strips of dead palm fronds, and the nest cups were lined with fine grasses. A snake skin was used as part of the nest cup lining in nest 1.

The dimensions ($\bar{x}$ ± SD) of nests 1, 7, and 8 were recorded. Mean exterior nest height was 145.0 mm ± 5.0. Mean exterior nest widths were 156.7 mm ± 23.1 front-to-back and 205.0 mm ± 21.2 side-to-side. Mean interior nest height was 72.5 mm ± 10.6. Mean inside height of the nest cup was 32.5 mm ± 3.5, while the mean inside widths were 69.3 mm ± 18.3 front-to-back and 57.5 mm ± 3.5 side-to-side. Mean entrance height was 47.5 mm ± 17.7, and mean entrance width was 46.7 mm ± 11.5.

Both males and females were observed

FIG. 1. Nest of the Black-bellied Wren, Soberania National Park, Republic of Panama, 16 July 2004. Photograph by S. K. Auer.

building nests (*n* = 5). On 10 May 2004, nest 7 was observed during the initial stages of construction for approximately 45 min. The nest base and rough shell of the dome structure had been completed at this stage. Only the male was observed building. The male sang at a high rate, singing 1–2 times each time he left the nest in search of new material. The nest cup was fully lined and appeared complete 5 days later on 15 May 2004. Nests 1 and 4 were observed for 2 hrs on 15 June 2001 and 27 June 2002, respectively. Both nests had a base and partially completed dome. Only males were observed building, and females were not seen or heard in the vicinity of both nests. However, 5 days later and during a brief observation of nest 4 on 2 July 2002, the female was observed bringing fine lining material to the nest during the final stages of construction. The female of nest 2 on 6 July 2002 was also seen collecting lining material for the nest. Nest 8 was observed on 13 June 2004 for approximately 30 min when the nest cup was being lined. The male sang from the nest or accompanied the female while she collected lining material.

Egg Laying, Eggs, and Incubation..—Egg laying began 1–2 days after the female was last observed lining the nest (nests 2, 4, and 8). Eggs were laid on consecutive days. Egg color varied from creamy to beige with faint to dark brown speckles that were more concentrated at the blunt end (Fig. 2). Egg mass averaged 2.5 g ± 0.1 SD (*n* = 6 eggs, 2 clutches). Mean egg length and maximum width were 20.8 mm ± 0.6 SD (*n* = 12, 4 clutches) and 15.3 mm ± 0.4 (*n* = 12, 4 clutches), respectively. Clutch size was three for all five nests found during the nest building stage and monitored through the laying period. Of the two nests found during the nestling stage, one had three nestlings (nest 3) and the other (nest 9) was depredated before we could count the nestlings.

Morning incubation behavior of radio-marked pairs was recorded for nest 6 on 28 April, 30 April, 2 May, and 3 May 2003 during unknown stages of incubation. Incubation behavior at nest 5 was recorded on 19 July, 22 July, and 26 July 2004 which corresponded to 9–10, 6–7, and 2–3 days before hatching, respectively. Nest attentiveness (% time at nest) ranged from 23 to 71% across observation periods of the two females. Females spent an average of 37% ± 17 SD (*n* = 7 days) of the observation time at the nest. Mean duration of time that females spent at and away from the nest was 45 min ± 23 (*n* = 9) and

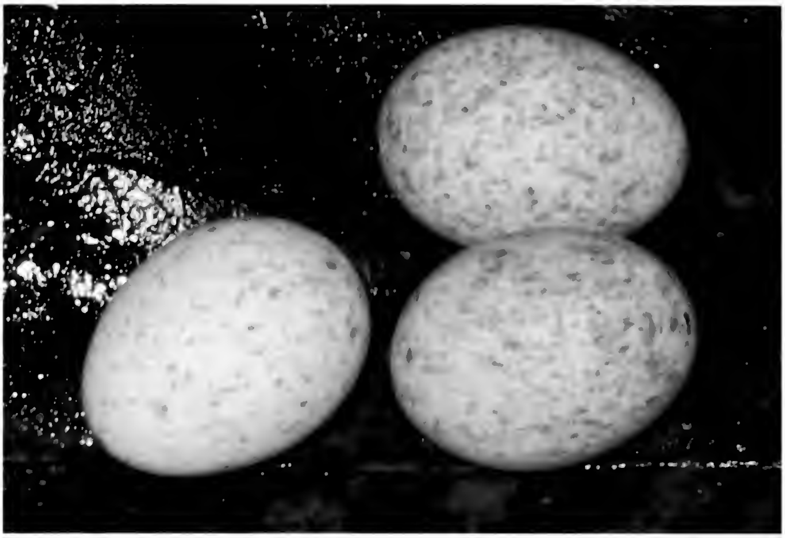

FIG. 2. Eggs of the Black-bellied Wren, Soberania National Park, Republic of Panama, 19 May 2004. Photograph by S. K. Auer.

40 min ± 19 SD ($n = 7$), respectively. Males were observed to visit the nest 0–2 times per observation session and spent an average of 11 min ± 7 SD ($n = 5$ visits) at the nest. Only three trips were made by males visiting their females at the nest of five total male visits summed across the two nests. It was not possible to ascertain if males were delivering food to their mates during these three trips. During the other two visits, males arrived at the nest while the females were away, remained there alone for 3 and 7 min, and then left shortly after the female arrived. Females of both pairs were observed at the nest prior to sunrise, suggesting they remained at the nest overnight.

Incubation behavior at nest 7 was filmed from 0710 to 1350 hrs on 20 May 2004, a day after the last egg was laid. During this time, the female incubated the eggs for only two sessions. Duration of the first on-bout was 62 min. The second on-bout lasted 31 minutes before recording was terminated by the end of the video. The female spent 25% of the video session incubating the eggs during which she was fed three times by the male. The male sang at a high rate, singing 4–5 times while approaching and leaving the nest.

Nestlings.—Nest 9 was observed during the nestling period for approximately 30 min on 3 July 2004. During this time, only the female brooded the nestlings, but both male and female provisioned the nestlings with arthropods. On 10 July 2002, nest 3 was observed for 1.5 hrs during the nestling phase. Both the male and female were observed feeding the nestlings.

Nest Success.—Nest 3 fledged all three young. Nest 5 was depredated 1–2 days after hatching. Nest 6 (whose nest contents could not be observed directly due to its location) was attended for at least 8 days and then abandoned, suggesting depredation. Nest 7 was depredated during the incubation period, 1–7 days after the last egg was laid. Nest 8 was also depredated during the incubation period and 1–3 days after the last egg was laid. One to 5 days after their pin feathers first emerged, nestlings disappeared from nest 9. The nest was found ripped up.

DISCUSSION

Nests of the Black-bellied Wren in Panama were similar in structure to those described in other locations (Hilty 1977, Stiles and Skutch 1989) and to the dome-shaped structures common in *Thryothorus* wrens (Skutch 1960, Brewer 2001). They were most similar to nests described for the Plain Wren (*T. modestus*), Rufous-breasted Wren (*T. rutilus*), Sooty-headed Wren (*T. spadix*), and Whiskered Wren (*T. mystacalis*). All five species construct globular nests with a circular side entrance and a reduced or absent antechamber relative to those of their congeners (Skutch 1960, Brewer 2001).

Nest sites tended to be low and in tangled vegetation near a forest edge. Pairs with territories in the forest interior nested near natural gaps such as bodies of water, while those with territories near forest borders readily built their nests near anthropogenic edges including roads and artificial forest clearings. Selection of nest sites in vine tangles is similar to that described for the Rufous-breasted and Plain wrens, but all three species show variability in nest site selection (Skutch 1960, Stiles and Skutch 1980).

Parental roles of males and females differed during the building stage. Females were observed to contribute only during later stages when the nest cup was being lined. Variation in the involvement of males and females across phases of nest construction may reflect biases due to our infrequent observations, or they may reflect real differences in male and female roles during this stage. In some tropical wrens, males and females take equal part in building during all stages of construction (Skutch 1960, Brewer 2001, Gill and Stutchbury 2005). However, in other species, including the congeneric Carolina Wren (*Thyrothorus ludovicianus*) and Winter Wren (*Troglodytes troglodytes*), males are often involved in the early and middle stages of nest construction while females complete the final phase of construction (Armstrong 1955, Skutch 1960, Brewer 2001).

Our data indicate that only the female incubates. We also observed that brood patches were apparent on 70% of adult females mist-netted between April and August 2001–2004 (n = 46), while only 3% of adult males showed thin feathering in the brood patch area during this period (n = 66; DML, unpubl. data). Incubation is performed only by the female in most wrens studied, and it is probable this is also the case in the Black-bellied Wren (Skutch 1960, Brewer 2001).

Males assisted females by feeding them at the nest although they did not incubate. Incubation feeding in *Thryothorus* has been reported only in the Carolina Wren, and evidence within the larger wren family is limited mostly to other North American species (Brewer 2001). Information on incubation behavior in many tropical wrens is lacking and it is unclear if incubation feeding is primarily a northern climate phenomenon.

Many characteristics of the breeding biology and behavior of Black-bellied were comparable to several congeners, generally including similarities in their domed nest structures, preference for nest sites in vine tangles, and the roles of males and females during different stages of the nesting cycle. We also found new evidence for incubation feeding in a tropical species of *Thryothorus*. However, additional studies of the breeding biology and behavior of the Black-bellied Wren are necessary to better understand the diversity of nest sites used, duration of the incubation and nestling periods, male incubation feeding rates, nest success, predation rates, and extent of fledgling care.

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SEASONAL BIRD USE OF CANOPY GAPS IN A BOTTOMLAND FOREST

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ABSTRACT.—Bird use of small canopy gaps within mature forests has not been well studied, particularly across multiple seasons. We investigated seasonal differences in bird use of gap and forest habitat within a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. Gaps were 0.13- to 0.5-ha, 7- to 8-year-old group-selection timber harvest openings. Our study occurred during four bird-use periods (spring migration, breeding, postbreeding, and fall migration) in 2001 and 2002. We used plot counts and mist netting to estimate bird abundance in canopy gaps and surrounding mature forest habitats. Using both survey methods, we observed more birds, including forest-interior species, forest-edge species, field-edge species, and several individual species in canopy gap and gap-edge habitats than in surrounding mature forest during all periods. Interactions between period and habitat type often were significant in models, suggesting a seasonal shift in habitat use. Bird activity generally shifted between the interior of canopy gaps and the immediate gap edge, but many species increased their use of forested habitat during the breeding period. This suggests that many species of birds selectively choose gap and gap-edge habitat over surrounding mature forest during the non-breeding period. Creation of small canopy gaps within a mature forest may increase local bird species richness. The reasons for increased bird activity in gaps remain unclear. *Received 8 August 2005. Accepted 12 July 2006.*

Many species of birds, including several species of conservation concern that breed in mature forests, require some amount of forest disturbance to create ideal habitat (Hunter et al. 2001). One type of disturbance common in mature forests occurs when trees fall from fire, ice, wind, or insect damage creating small light gaps in the forest canopy. Such gaps provide microclimates and habitat patches that lead to a unique assortment of gap-associated flora and fauna (Watt 1947, Canham et al. 1990), and increase the heterogeneity of vegetation structure in the forest. Canopy gaps created by small-scale timber harvest operations may mimic these natural disturbances.

Birds select habitat based largely upon vegetation structure (Holmes et al. 1979), and some may prefer early successional gap habitat based on the unique qualities of the vegetation (e.g., dense foliage, well-developed herb and shrub layer). Several bird species seem to prefer small-scale canopy gap openings to mature forested habitat during migration or the breeding period (Martin and Karr 1986, Germaine et al. 1997, Kilgo et al. 1999, Moorman and Guynn 2001). Forest canopy gaps may be used differently throughout the year, depending on the availability of protective cover, desirable nesting habitat, or suitable prey items (Robinson and Holmes 1982, Willson et al. 1982, Blake and Hoppes 1986). During migration, birds pass through unfamiliar habitats and tend not to spend much time in any one location (Moore et al. 1993). Habitat selection during these periods may be influenced by available food resources, competition with other species, and risk of predation (Petit 2000). During the breeding period, birds require habitat with suitable nesting sites. Birds that breed in early successional habitats, including Common Yellowthroat and Indigo Bunting (scientific names in Appendix), use regenerating canopy gaps for nesting (Moorman and Guynn 2001). During the postbreeding period, adults may select densely vegetated habitats as refugia while molting (Vega Rivera et al. 1999), and young may seek the protective cover from predators offered by gaps (Anders et al. 1998, Vega Rivera et al. 1998), as each group is particularly vulnerable at that time.

Seasonal variation in the use of artificial, small-scale disturbances by birds within mature forests has not been well studied, and no research has systematically addressed the relative use of gap habitat throughout the growing season, beginning with spring migration

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and ending with fall migration. Our goal was to examine relative use of gap and forest habitat by birds through four periods (spring, breeding, postbreeding, and fall) within a bottomland hardwood forest to provide a more comprehensive assessment of the response of forest birds to canopy gaps. We hypothesized that relative bird use of gaps would be highest during the non-breeding period when dense vegetative cover is important to dispersing and migrating individuals.

METHODS

Study Area.—We studied birds during 2001 and 2002 at the Savannah River Site (33° 09′ N, 81° 40′ W), a 78,000-ha National Environmental Research Park owned and operated by the U.S. Department of Energy. Our study site was a mature stand of bottomland hardwoods approximately 120 ha in size in Barnwell County in the Upper Coastal Plain of South Carolina. We surveyed birds in 12 group-selection gaps harvested in December 1994 and in the mature forest adjacent to gaps. Gaps were of three sizes (0.13, 0.26, and 0.50 ha) with four replicates of each size. It is within this size range that previous research has identified a threshold in response by breeding (Moorman and Guynn 2001) and fall migrant birds (Kilgo et al. 1999). The mature forest canopy was dominated by laurel oak (*Quercus laurifolia*), cherrybark oak (*Q. falcata* var. *pagodaefolia*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*). The midstory was poorly developed, consisting primarily of red mulberry (*Morus rubra*), ironwood (*Carpinus carolinianus*), and American holly (*Ilex opaca*). The understory was dominated by dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*). Vegetation in the gaps was approximately 1–8 m in height and was dominated by regenerating trees (primarily sweetgum, loblolly pine, sycamore [*Platanus occidentalis*], green ash [*Fraxinus pennsylvanica*], oaks, and black willow [*Salix nigra*]), and dense stands of blackberry (*Rubus* spp.), dwarf palmetto, and switchcane.

Bird Surveys.—We surveyed birds each year during four avian activity periods: spring migration (25 Mar through 15 May), breeding (16 May through 30 Jun), postbreeding (1 Jul through 31 Aug), and fall migration (1 Sep through 18 Oct). These beginning and ending dates are estimates of biologically meaningful periods, but each overlaps extensively with the other. Although many individuals initiated breeding on our study area before 16 May, transient species that breed to the north continued to migrate through South Carolina until mid-May. Similarly, some individuals migrated from or through our study area before 1 September, but the bulk of fall migration occurred after 1 September.

Plot counts were conducted within each of the 12 experimental gaps and within 12 forested control plots of equivalent size. The 12 forested control plots were randomly placed a minimum of 100 m from the nearest gap center within the mature forest surrounding the study gaps. The forest plot perimeters were flagged so that observers could easily identify plot boundaries. Each of the 24 plots was visited three times during each period and counts were averaged over the three visits. For approximately one half of the plot counts and equally distributed across treatment types, two observers walked slowly around the perimeter of each plot, recording all birds seen and heard. When the observers met on the opposite side of the plot, they compared observations and agreed upon a total number for each bird species observed within the gap-edge habitat. When only one observer was available, the single observer walked slowly around the entire plot. At both forest and gap plots, birds observed within the actual plot and at the immediate edge (0–10 m from the bole line or flagged boundary into the forest) were included in the count. Surveys varied widely in length (15 to 45 min); larger plots and plots with more bird activity took longer to survey. The percentage of gap habitat in plot counts increased as gap size increased. However, the effect of gap size on bird use was not significant ($P > 0.05$) and we did not include the variable in our models.

At each of the 12 study gaps, we placed three constant effort mist-net stations along a line emanating southward from the gap center: one at the approximate gap center, one at the gap edge perpendicular to and bisecting the tree line, and one 50 m into the surrounding forest. The interior gap mist net was a proxy for gap abundance, the gap-edge net was a proxy for edge abundance, and the 50-m-into-the-forest net was a proxy for forest abundance. During the spring migration, postbreeding, and fall migration periods, netting was conducted once each week at each gap, rotating among gaps on a regular weekly schedule. During the breeding period, nets were operated once every 2 weeks because birds tend to remain fairly stationary during this period. Nets were opened at first light and operated for 4–6 hrs, depending on daily weather conditions. Netting was not conducted when wind exceeded 16 km/hr or during steady rainfall. Nets were 12 m long × 3 m tall, with 30-mm mesh. Captured birds were classified to age and gender (Pyle 1997), weighed, and banded with a federal aluminum leg band. We operated mist nets for a total of 7,669 net hrs over the 2 years of the study.

Mist-net surveys and plot counts were not meant to be directly comparable, but rather separate, distinct measures of bird use of gap and adjacent forest habitat in each of four bird-use periods. Plot counts at gap sites included both gap and edge habitat, so the percentage of bird use of gap *per se* versus the first 10 m of forest (i.e., the edge) could not be measured seasonally as it could for mist-net captures. We chose not to note whether birds specifically were recorded in the 10-m outer band of gap and control plot counts because birds often moved back and forth across the boundary as they foraged. Additionally, we were most interested in bird use of gap-edge habitat compared to an equal size area of mature forest. Finally, forest mist-net stations were not placed with control plot count circles because the best location (i.e., at least 100 m from the nearest gap center) for plot counts frequently did not lie along the southward emanating mist-net transect. Mist nets and plot counts each have their limitations, but the combined use of the two sampling techniques allowed us to more comprehensively measure bird use of the gaps and adjacent mature forest.

Statistical Analyses.—We used a linear mixed model (PROC MIXED, SAS Institute, Inc. 1990) to perform repeated measures ANOVA comparing the effects of habitat type, period, and the interaction between habitat and period on bird abundance. We used mean birds per ha as the dependent variable for plot count analyses and mean captures per 100 net hrs as the dependent variable for mist-netting analyses. For plot count data analysis, habitats included gap-edge and forest; for mist-netting data analysis, habitats included gap, edge, and forest. We considered habitat type and period as fixed effects, with habitat type as a split plot factor and period as the repeated measure. We used the test for the habitat × period interaction to assess whether habitat use was consistent across periods (i.e., an interaction between the two variables indicated that relative use of the habitats differed among the periods). Significant interactions generally were the result of varying extents of differences among gap, edge, and forest use but in a consistent direction across periods. We interpreted period and habitat effects separately even when there was an interaction between the two variables. Years were not significant ($P > 0.05$) in any model and were pooled in the final analyses. These pooled data are represented in tables and figures.

We assigned birds to habitat-use groups (Appendix): (1) all birds, (2) forest-interior species, (3) forest-edge species, and (4) field-edge species (Ehrlich et al. 1988, Hamel 1992). We analyzed mist-netting captures and plot count detections for each group. Individual species were chosen for analysis if they accounted for at least 80 detections over both years for plot counts (Blue-gray Gnatcatcher, Carolina Wren, Tufted Titmouse, Northern Cardinal, Northern Parula, and White-eyed Vireo) or at least 80 captures over both years for mist netting (Black-throated Blue Warbler, Carolina Wren, Hooded Warbler, Kentucky Warbler, Northern Cardinal, and White-eyed Vireo). We included species that bred at our study site and transient migrants that bred to the north in our analyses. Birds considered winter residents, present only in early spring or late fall, were not included.

RESULTS

Plot Counts.—From April through October in 2001 and 2002, we counted 1,711 individuals representing 70 species in gap-edge habitat and 38 species in forest habitat. We detected more individuals in the gaps than in the surrounding forest during all periods for all bird groups and individual species analyzed (Table 1, Fig. 1). The abundance of forest-interior birds, field-edge birds, Blue-gray

TABLE 1. Effects of period (spring migration, breeding, postbreeding, fall migration), habitat (gap-edge and forest), and the period × habitat interaction (ANOVA) on abundance of bird species/groups detected on plot counts of gaps and forest areas in a bottomland hardwood forest in South Carolina, 2001–2002.

	Period			Habitat			Period × habitat		
Species or group	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
All birds	1.00	3,162	0.40	49.71	1,22	<0.001	0.66	3,162	0.58
Forest interior species	4.94	3,162	0.003	24.05	1,22	<0.001	0.83	3,162	0.48
Forest-edge species	2.10	3,162	0.10	60.16	1,22	<0.001	0.50	3,162	0.68
Field-edge species	27.55	3,162	<0.001	85.05	1,22	<0.001	27.90	3,162	<0.001
Blue-gray Gnatcatcher	14.08	3,162	<0.001	42.82	1,22	<0.001	5.80	3,162	0.001
Carolina Wren	9.44	3,162	<0.001	83.17	1,22	<0.001	1.76	3,162	0.16
Tufted Titmouse	12.78	3,162	<0.001	18.70	1,22	<0.001	2.22	3,162	0.088
Northern Cardinal	4.60	3,162	0.004	32.76	1,22	<0.001	0.60	3,162	0.61
Northern Parula	9.63	3,162	<0.001	19.43	1,22	<0.001	2.65	3,162	0.052
White-eyed Vireo	1.82	3,162	0.15	30.56	1,22	<0.001	1.49	3,162	0.22

Gnatcatcher, Carolina Wren, Tufted Titmouse, Northern Cardinal, and Northern Parula differed among periods, but no consistent patterns were evident, as seasonal use varied considerably by species or group (Table 1, Fig. 1).

Interactions between period and habitat type existed for field-edge birds, Blue-gray Gnatcatcher, and Northern Parula (Table 1). Field-edge birds were detected most often during spring and fall migration and primarily in gap-edge habitat (Fig. 1). The greatest proportion of forest detections of field-edge birds occurred during the postbreeding period. The Blue-gray Gnatcatcher was most abundant in gap-edge habitat during all periods, but forest detections decreased to almost zero during fall migration (Fig. 1). Northern Parula used both gap-edge and forest habitat during spring migration and the breeding period, but almost all detections were in gap-edge during the postbreeding period and fall migration (Fig. 1).

Mist Netting.—From April through October in 2001 and 2002, we captured 1,476 birds representing 56 species. We captured 55 species in gap and edge habitat, and 26 species in forest habitat across all periods. We captured more individuals in the gaps and at their edges than in the surrounding forest during all periods for all bird groups and individual species except the Carolina Wren, which was captured more frequently at edge or forest habitats than gaps during all periods (Table 2, Fig. 2). Number of captures differed among periods for all groups and species analyzed except Kentucky Warbler and Northern Cardinal, with most groups being most frequently captured during spring migration (Table 2, Fig. 2).

There was an interaction between period and habitat type, indicating a seasonal shift in habitat use, for all birds, forest-interior birds, forest-edge birds, field-edge birds, Black-throated Blue Warbler, Carolina Wren, Hooded Warbler, Kentucky Warbler, and White-eyed Vireo (Table 2). Some species (e.g., forest-interior specialists and Kentucky Warbler) shifted from gap during spring migration to edge during the breeding period and back to gap habitat after the breeding period (Fig. 3). Forest-edge birds were most abundant in the gap habitat during spring and fall migration, but both gap and edge were used equally during the breeding and postbreeding periods. Total mist-net captures tended to shift slightly between gap and edge habitat (gap during spring and fall migratory periods, edge during breeding and postbreeding), with forest captures representing just a small proportion of captures during each period. The highest proportion of forest captures, however, occurred during the breeding period (Fig. 3). Forest-interior birds, forest-edge birds, Carolina Wren, and Hooded Warbler used forested habitat most during the breeding period (Fig. 3).

DISCUSSION

We observed and captured more birds in gap and gap-edge habitat than in the surrounding mature forest during all bird-use periods. Generally, bird detections in edge habitat were more similar to detections in gap habitat than mature forest habitat. The Carolina Wren was

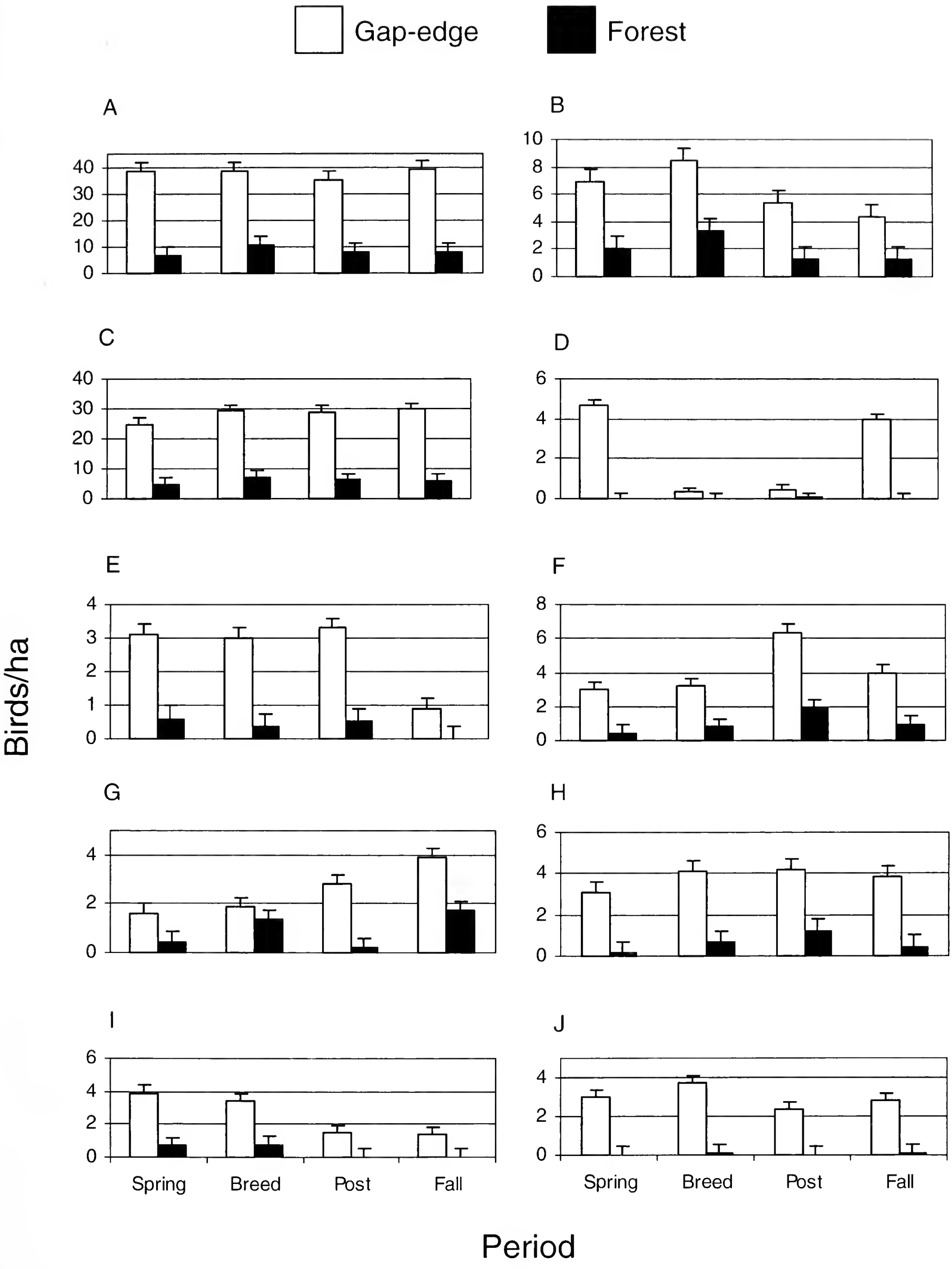

FIG. 1. Seasonal plot counts (mean birds/ha) for gap-edge (open bars) and forest habitats (filled bars), with standard error bars (2001 and 2002 in South Carolina). (A) all birds, (B) forest-interior species, (C) forest-edge species, (D) field-edge species, (E) Blue-gray Gnatcatcher, (F) Carolina Wren, (G) Tufted Titmouse, (H) Northern Cardinal, (I) Northern Parula, and (J) White-eyed Vireo.

TABLE 2. Effects of period (spring migration, breeding, postbreeding, fall migration), habitat (gap, edge, forest), and the period × habitat interaction (ANOVA) on the number of mist-net captures for bird species/groups in a bottomland hardwood forest in South Carolina, 2001–2002.

Species or group	Period			Habitat			Period × habitat		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
All birds	36.93	3,33	<0.001	43.99	2,33	<0.001	16.05	6,33	<0.001
Forest-interior species	21.87	3,33	<0.001	19.62	2,33	<0.001	6.82	6,33	<0.001
Forest-edge species	15.27	3,33	<0.001	22.45	2,33	<0.001	4.06	6,33	0.004
Field-edge species	36.94	3,33	<0.001	21.38	2,33	<0.001	7.37	6,33	<0.001
Black-throated Blue Warbler	8.64	1,66	0.005	17.91	2,66	<0.001	3.59	2,66	0.033
Carolina Wren	3.85	3,132	0.011	9.64	2,132	<0.001	1.96	6,132	0.076
Hooded Warbler	6.86	3,132	<0.001	14.73	2,132	<0.001	1.96	6,132	0.075
Kentucky Warbler	2.27	2,99	0.11	7.70	2,99	<0.001	5.50	4,99	<0.001
Northern Cardinal	2.25	3,132	0.085	12.65	2,132	<0.001	1.01	6,132	0.42
White-eyed Vireo	5.05	3,132	0.002	22.86	2,132	<0.001	1.83	6,132	0.098

the only species to show a distinct forest/edge preference, based on mist-netting captures. Other studies have reported more bird activity in early successional habitats than mature forest, including migrating foliage gleaning insectivores (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986, Kilgo et al. 1999), breeding birds (Smith and Dallman 1996, Germaine et al. 1997, King et al. 2001, Moorman and Guynn 2001), and postbreeding birds (Anders et al. 1998; Vega Rivera et al. 1998, 1999, 2003; Pagen et al. 2000). Migrating birds also may prefer forest-edge habitat to forest-interior habitat during fall migration (Rodewald and Brittingham 2002). Other researchers have found that individual species, including Hooded Warbler (Annand and Thompson 1997, Robinson and Robinson 1999), Carolina Wren (Robinson and Robinson 1999, Moorman and Guynn 2001), and White-eyed Vireo (Robinson and Robinson 1999, Moorman and Guynn 2001) use regenerating group-selection openings more than mature forest during the breeding period. Hooded Warblers nest (Moorman et al. 2002) and forage (Kilgo 2005) in the mature forest understory on our site, but often were seen foraging in the gap habitat during all periods, and with young in gap habitat during the postbreeding period (LTB, pers. obs.).

It is possible that we captured more birds in gap habitat than forest habitat because of differences in habitat structure (Remsen and Good 1996). Birds using the low vegetation within the gaps were more available for sampling with a 3-m tall net than birds in the mature forest. However, our plot counts corroborated our mist-net data; they sampled both the understory and canopy, and also detected more birds using gap habitat than mature-forest habitat. Plot counts included birds using the immediate edge of gaps, a mix of habitat types and vegetation structures, which may have attracted forest-interior birds more than the actual gap center. Ease of detection of birds in gaps during plot counts likely was lower than in the forest because of the dense vegetation in the gaps and our estimates of bird use of gaps may be conservative.

While most birds used gap and edge habitat more than forested habitat during all periods, we also detected a seasonal shift in habitat use for several groups, as evidenced by interac-

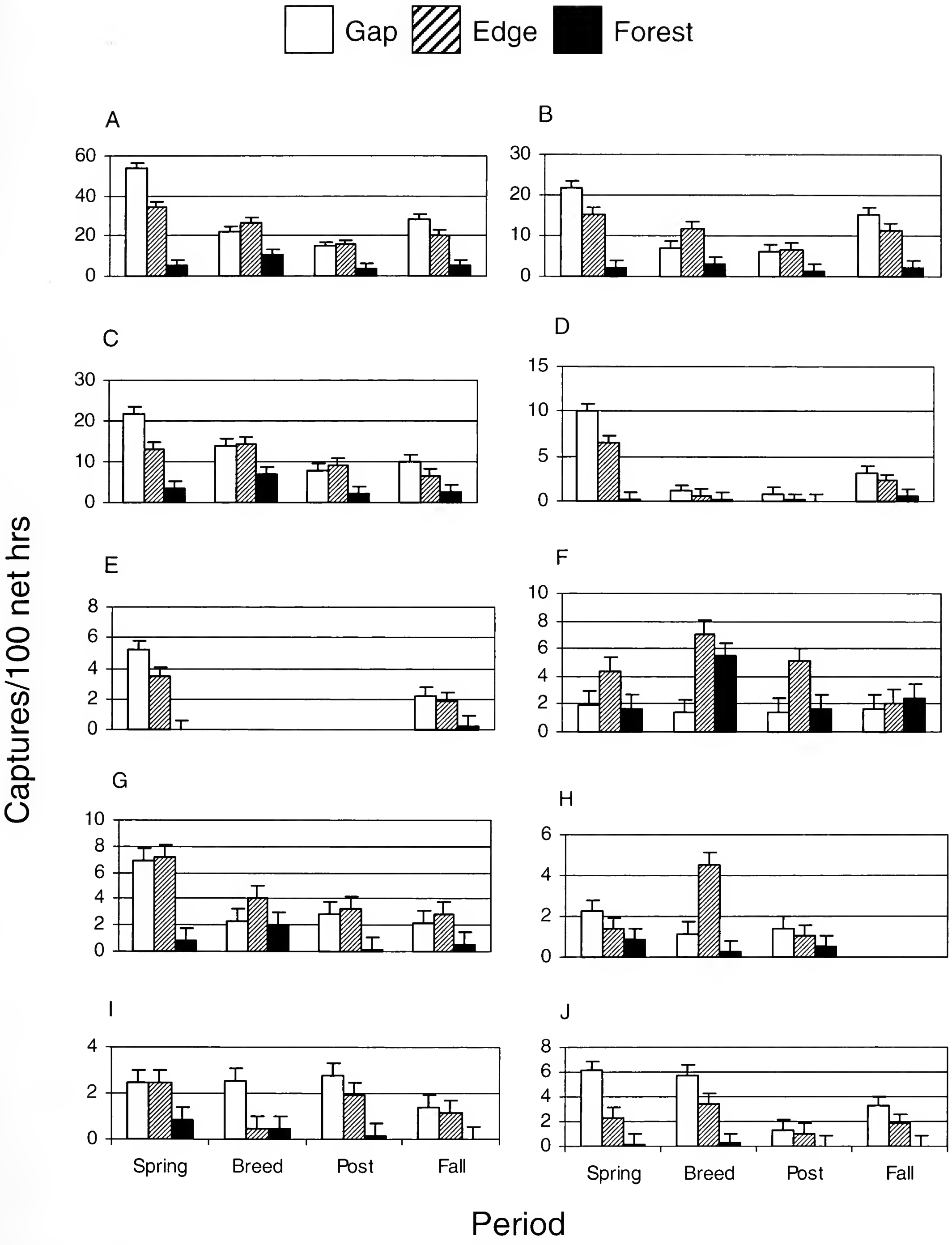

FIG. 2. Mean bird captures/100 net hrs for each habitat and period with standard error bars (2001 and 2002 in South Carolina). (A) all birds, (B) forest-interior species, (C) forest-edge species, (D) field-edge species, (E) Black-throated Blue Warbler, (F) Carolina Wren, (G) Hooded Warbler, (H) Kentucky Warbler, (I) Northern Cardinal, and (J) White-eyed Vireo.

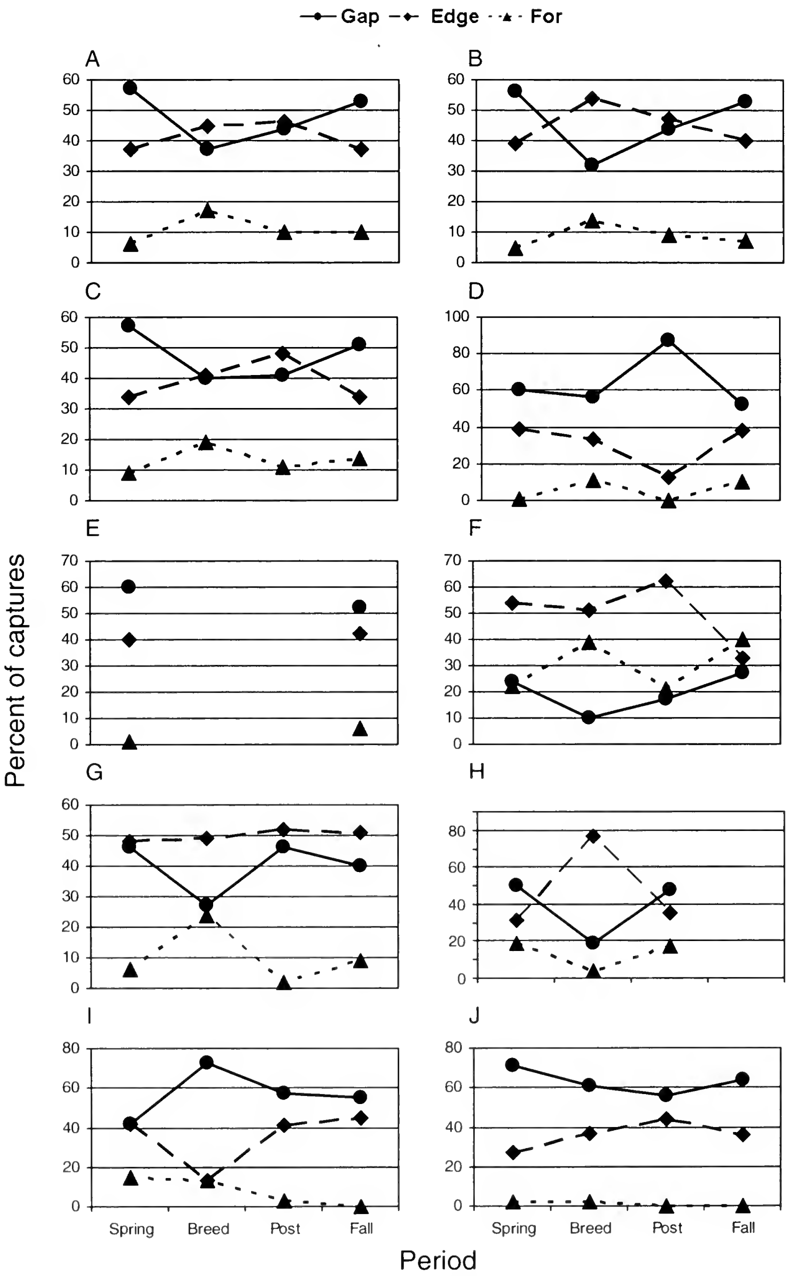

FIG. 3. Percent of mist-net captures per period occurring in each habitat type (gap, edge, forest) in a bottomland forest (2001 and 2002 in South Carolina). (A) all birds, (B) forest-interior species, (C) forest-edge species, (D) field-edge species, (E) Black-throated Blue Warbler, (F) Carolina Wren, (G) Hooded Warbler, (H) Kentucky Warbler, (I) Northern Cardinal, and (J) White-eyed Vireo.

tions between period and habitat; the relative proportions of gap, edge, and forest captures varied among periods. Generally, bird use of gap and edge habitats was highest during spring and fall migration, while use of forested habitat tended to be greatest during the breeding period and lowest during the migratory periods. Other research has documented seasonal shifts in habitat use between the breeding and postbreeding periods, particularly as fledgling birds moved from forested habitat into early- and mid-successional habitats (Anders et al. 1998; Vega Rivera et al. 1998, 2003; Pagen et al. 2000), possibly in search of greater cover or more abundant food resources. Regenerating forest canopy gaps may provide a necessary habitat type for birds during seasons of increased mobility.

Gap interiors were not only densely vegetated, but also contained early successional fruiting species (e.g., winged sumac [*Rhus copallina*] and blackberry), while other fruiting species such as poison ivy (*Toxicodendron radicans*) and hawthorn (*Crataegus* spp.) were common at the immediate gap edge (LTB, pers. obs.). We observed omnivorous birds eating fruits in gaps, including American beautyberry (*Callicarpa americana*), flowering dogwood (*Cornus florida*), grape (*Vitis* sp.), hawthorn, poison ivy, and winged sumac (LTB, pers. obs.). Fruit typically is most abundant from late summer through early fall (McCarty et al. 2002). Willson et al. (1982) reported that avian frugivores preferentially visited natural forest openings during migratory periods, even when these gaps provided no more fruit than surrounding forest habitat. We did not, however, find a corresponding shift in habitat use for omnivorous species such as Northern Cardinal, suggesting that birds were meeting their nutritional needs without closely following seasonal fruit availability.

Birds used regenerating canopy gaps more than mature forested habitat during all periods. Bird habitat use shifted slightly from gaps during spring migration to forest during the breeding period, then back to gaps during the postbreeding period and fall migration. Reasons for these habitat selections and seasonal shifts, however, remain speculative. It is possible that omnivorous birds use canopy gaps more during periods of high fruit availability, as canopy gaps are known for their high fruit abundance (Levey 1990). However, fruit production within our canopy gaps was relatively low and highly seasonal, with no fruit available during spring, one of the periods of highest bird use. We suspect birds may select regenerating canopy gaps for the protection offered by these densely vegetated areas, particularly during periods of vulnerability, such as during migration when birds move through unfamiliar areas and during the postfledging period when young are more vulnerable to predators. Alternatively, birds could be tracking seasonal changes in the abundance of arthropod food resources, if the relative abundance of arthropods in gaps and forest habitat changes through the year. Additional work is needed to assess the relative importance of vegetation structure and arthropod abundance in affecting seasonal avian habitat use in southeastern forests.

The creation of 0.13- to 0.5-ha canopy gaps can increase habitat diversity within mature bottomland hardwood forest, thereby attracting a greater number of foraging, breeding, and migrating birds. This practice may be particularly beneficial in stands with a sparse understory because of dense canopy closure, a condition common to the mid-successional forests that dominate the southeastern United States. Our gaps did not impact reproductive success of Hooded Warblers nesting in the surrounding forest (Moorman et al. 2002), probably because of the extensive amount of forest cover in the landscape (i.e., the extent of forest fragmentation is low). Further, Robinson and Robinson (1999) noted that long-term effects of small-scale canopy gaps on the forest bird community are unlikely because the regenerating forest matures and returns to pre-harvest conditions in a relatively short time. When the gaps we studied were 2–5 years old (Kilgo et al. 1999, Moorman and Guynn 2001), their contrast with the surrounding forest, in terms of vegetation height and structure, was dramatic. During the current study, the gaps were 7–8 years old and the contrast was beginning to blur, with many gaps more closely resembling the surrounding forest than 3-year-old gaps; some saplings exceeded 10 m in height.

Group-selection timber harvest could allow generation of income concurrent with an increase in habitat diversity, especially in forests where rates of natural canopy-gap creation have been altered by prior human disturbance (e.g., fire suppression, even-aged timber harvest, altered flooding regimes). Pashley and Barrow (1993) recommended a management regime that mimics natural disturbance to maintain habitat heterogeneity. Our results highlight the importance of this recommendation, as birds used both forested and early successional habitat at different times during the year.

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IAPPENDIX. Observed bird species and their habitat group associations. Species included were detected by plot counts or mist-netting at least once (South Carolina, 2001–2002).

Species	Scientific name	Habitat group
Turkey Vulture	*Cathartes aura*	field edge
Red-shouldered Hawk	*Buteo lineatus*	forest edge
Mourning Dove	*Zenaida macroura*	field edge
Yellow-billed Cuckoo	*Coccyzus americanus*	forest edge
Barred Owl	*Strix varia*	forest interior
Ruby-throated Hummingbird	*Archilochus colubris*	forest edge
Red-headed Woodpecker	*Melanerpes erythrocephalus*	forest edge
Red-bellied Woodpecker	*Melanerpes carolinus*	forest edge
Downy Woodpecker	*Picoides pubescens*	forest edge
Hairy Woodpecker	*Picoides villosus*	forest interior
Northern Flicker	*Colaptes auratus*	forest edge
Pileated Woodpecker	*Dryocopus pileatus*	forest interior
Eastern Wood-Pewee	*Contopus virens*	forest edge
Acadian Flycatcher	*Empidonax virescens*	forest interior
Eastern Phoebe	*Sayornis phoebe*	forest edge
Great Crested Flycatcher	*Myiarchus crinitus*	forest edge
White-eyed Vireo	*Vireo griseus*	forest edge
Yellow-throated Vireo	*Vireo flavifrons*	forest edge
Blue-headed Vireo	*Vireo solitarius*	forest interior
Red-eyed Vireo	*Vireo olivaceus*	forest interior
Blue Jay	*Cyanocitta cristata*	forest edge
American Crow	*Corvus brachyrhynchos*	forest edge
Fish Crow	*Corvus ossifragus*	forest edge
Carolina Chickadee	*Poecile carolinensis*	forest edge
Tufted Titmouse	*Baeolophus bicolor*	forest edge
White-breasted Nuthatch	*Sitta carolinensis*	forest edge
Brown-headed Nuthatch	*Sitta pusilla*	forest edge
Carolina Wren	*Thryothorus ludovicianus*	forest edge
Blue-gray Gnatcatcher	*Polioptila caerulea*	forest edge
Veery	*Catharus fuscescens*	forest interior
Gray-cheeked Thrush	*Catharus minimus*	forest interior
Bicknell's Thrush	*Catharus bicknelli*	forest interior
Swainson's Thrush	*Catharus ustulatus*	forest interior
Hermit Thrush	*Catharus guttatus*	forest interior
Wood Thrush	*Hylocichla mustelina*	forest interior
Gray Catbird	*Dumetella carolinensis*	field edge
Brown Thrasher	*Toxostoma rufum*	field edge

APPENDIX. Continued.

Species	Scientific name	Habitat group
Blue-winged Warbler	*Vermivora pinus*	field edge
Golden-Winged Warbler	*Vermivora chrysoptera*	forest edge
Northern Parula	*Parula americana*	forest edge
Chestnut-sided Warbler	*Dendroica pensylvanica*	field edge
Magnolia Warbler	*Dendroica magnolia*	forest interior
Black-throated Blue Warbler	*Dendroica caerulescens*	forest interior
Yellow-rumped Warbler	*Dendroica coronata*	forest edge
Black-throated Green Warbler	*Dendroica virens*	forest interior
Pine Warbler	*Dendroica pinus*	forest edge
Prairie Warbler	*Dendroica discolor*	field edge
Black-and-white Warbler	*Mniotilta varia*	forest interior
American Redstart	*Setophaga ruticilla*	forest interior
Worm-eating Warbler	*Helmitheros vermivorum*	forest edge
Swainson's Warbler	*Limnothlypis swainsonii*	forest interior
Ovenbird	*Seiurus aurocapilla*	forest interior
Northern Waterthrush	*Seiurus noveboracensis*	forest interior
Louisiana Waterthrush	*Seiurus motacilla*	forest interior
Kentucky Warbler	*Oporornis formosus*	forest interior
Common Yellowthroat	*Geothlypis trichas*	field edge
Hooded Warbler	*Wilsonia citrina*	forest interior
Canada Warbler	*Wilsonia canadensis*	forest interior
Yellow-breasted Chat	*Icteria virens*	field edge
Summer Tanager	*Piranga rubra*	forest edge
Scarlet Tanager	*Piranga olivacea*	forest interior
Eastern Towhee	*Pipilo erythrophthalmus*	field edge
Northern Cardinal	*Cardinalis cardinalis*	forest edge
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	forest interior
Indigo Bunting	*Passerina cyanea*	field edge
Common Grackle	*Quiscalus quiscula*	field edge
Brown-headed Cowbird	*Molothrus ater*	forest edge

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ANNUAL RETURN RATES OF BREEDING GRASSLAND SONGBIRDS

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ABSTRACT.—We used reobservation of color-banded birds to index annual breeding site fidelity of four species of songbirds that nest in the northern mixed-grass prairie of northcentral Montana (1996–2005). Territorial males of Sprague's Pipits (*Anthus spragueii*), and Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows were located on five permanent study sites (1998–2004) and lured into mist-nets using tape broadcasts of conspecific songs and calls. The proportion reobserved was 5.3% ($n = 247$) across all banded adult males. Grasshopper Sparrows had the highest proportion of returns (8.9%), followed by Savannah Sparrows (5.4%), Baird's Sparrows (5.1%), and Sprague's Pipits (2.1%). Three nestling Savannah Sparrows were reobserved in subsequent years ($n = 193$), while no nestlings of the other species were reobserved ($n = 401$). Our return rates were low for all adults in comparison with typical reports of return rates for songbird species of woodland and shrubland habitats. Migratory nomadism may explain this phenomenon, where grassland migrants are opportunistic in site selection, rather than faithfully returning to potentially uninhabitable former breeding sites. *Received 20 December 2005. Accepted 9 August 2006.*

Breeding site-fidelity is defined as the tendency of a migratory bird to return to a previous breeding site. Numerous studies have documented strong breeding site-fidelity in some migratory birds (Gavin and Bollinger 1988, Green 1992, Murphy 1996, Porneluzi 2003), especially for those species that nest in shrubland and forested habitats (Porneluzi and Faaborg 1999, Gardali et al. 2000). The return of migratory birds to earlier breeding sites demonstrates remarkable orientation and suggests strong evolutionary benefits to returning to the same area to breed, particularly when successful breeding has occurred at a site in the past (Gavin and Bollinger 1988, Porneluzi 2003). However, the potential benefits of returning to previously successful breeding sites could be negated if nesting habitat is highly variable from year-to-year, possibly becoming unsuitable in some years.

Grasslands of the northern prairies are dynamic environments with fluctuating conditions that, depending on scale and feature, are unpredictable in time and space, creating a mosaic of habitat conditions (Ahlering 2005, Winter et al. 2005). This variability is due to many causes, including effects of lightning- and human-set fires (Higgins 1984), intense grazing by prairie dogs (*Cynomys* spp.), bison (*Bison bison*), and other ungulates (Kirsch and Kruse 1973) and, perhaps most importantly, widely fluctuating precipitation levels across years (Igl and Johnson 1999, Ahlering 2005). Alternating periods of drought and above-average precipitation result in fluctuations in the structure and floristics of grasslands, within and between years (Winter et al. 2005). Strong annual variation in breeding habitat conditions can cause tremendous shifts in local and regional bird population densities (Fretwell 1986, Igl and Johnson 1999, Winter et al. 2005). Evidence suggests that some grassland birds have adapted to this variability by exhibiting low site fidelity, often resulting in spectacular fluctuations in local population densities (Cody 1985, Igl and Johnson 1999, Winter et al. 2005). Many grassland bird species have evolved nomadic strategies for breeding site selection since habitat instability makes it potentially unprofitable, even for previously successful nesters, to return consistently to the same grassland breeding areas

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(Andersson 1980). Nomadism is defined as the tendency of adults and juveniles to move widely in response to resources that are patchy in time and space (Andersson 1980, Johnson and Grier 1988). Nomadic behavior is a selectively advantageous alternative to site-fidelity for grassland birds (Cody 1985), and is indicated by relatively low return rates, when compared with return rates of birds inhabiting more stable environments (e.g., shrublands and forests).

Site fidelity studies of grassland bird populations are largely restricted to eastern North America. Sedge Wrens (*Cistothorus platensis*, Herkert et al. 2001), Henslow's (*Ammodramus henslowii*, Herkert et al. 2002), Le Conte's (*A. leconteii*, Murray 1969), and Nelson's Sharp-tailed (*A. nelsoni*, Murray 1969) sparrows all had return rates that were lower ($\leq$13.5%) than those typically reported for woodland and shrubland nesting passerines. However, Bobolinks (*Dolichonyx oryzivorus*), whose return rates varied from 44 (n = 85) to 70% (n = 79) for adult males (Gavin and Bollinger 1988, Bollinger and Gavin 1989, Martin and Gavin 1995), have return rates that are more commensurate with shrub and forest dwelling species (Green 1992). Dickcissel (*Spiza americana*) also showed a tendency to return to former breeding sites in the center of their range (Fretwell 1986), with a return rate of 49% (n = 82) in Kansas (Temple 2002).

We investigated breeding songbird site fidelity in the mixed-grass prairie of northcentral Montana. Four co-occurring species were studied: Sprague's Pipits (*Anthus spragueii*), and Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows. Data on grassland birds in the northern Great Plains are relatively scarce; no other return rate studies have been published on Sprague's Pipits with only one study on Baird's Sparrows (Green 1992).

METHODS

Study Area.—Our study was conducted at Bowdoin National Wildlife Refuge (NWR) in Phillips County, northcentral Montana (48° 24′ N, 107° 39′ W; ~750 m elevation). Data were collected during summers of 1996–2004 on five permanently located sites (26–59 ha) 1.3–10.1 km apart, comprising 218 ha of flat to gently rolling native mixed-grass prairie. Blue grama (*Bouteloua gracilis*), needle-and-thread (*Stipa comata*), western wheatgrass (*Pascopyrum smithii*), and dense clubmoss (*Selaginella densa*) were the dominant herbaceous species. Shrubs were sparse and trees absent. Bowdoin NWR has not been grazed by cattle for $\geq$29 years. One study site was partially burned in 1994 and one site was prescribed burned in 2000; otherwise, no burning events have occurred since refuge documentation began in 1936.

Capture and Marking.—Known territorial adult males were lured into 30- or 36-mm mesh mist nets using tape playback recordings of conspecific song beginning in 1998 (Sogge et al. 2001). We used Sony TC-D5Pro II or Marantz PDM 430 cassette recorders amplified by an AmpliVox s805 Multimedia Amplifier, connected into two tweeters by 30–50 m of 16-gauge speaker cord. Speakers were placed on either side of a 12-m mist net within the territory of a target male. Tape playback of conspecific song was broadcast to draw the target male into the net. Carved wooden decoys were placed at the net as visual lures beginning in 2003.

Each individual captured was marked with a uniquely numbered federal aluminum band, plus three color bands whose colors were randomly selected. Sprague's Pipits were banded with a year cohort color band, and a color band denoting gender and age. Incidental females captured at the net were also banded. Nestlings were banded, beginning in 1996, with a year cohort color; processing occurred on day 7 or 8 post-hatch (Dieni and Jones [2003] describe nest searching methods). Gender for adults was assigned based on the presence of a cloacal protuberance for males or brood patch for females; gender of hatching-year birds could not be assigned.

Returns.—Field assistants identified the banding status of all observed individuals among target species during nest searching activities from May to August 1997–2005. All individuals of the target species were checked for bands either by capture of territorial males or visually using binoculars and spotting scopes on all study sites. In addition, the target species were also visually observed, or oc-

TABLE 1. Grassland bird banding at Bowdoin National Wildlife Refuge, Montana. Adult male banding effort from 1998 to 2004, nestlings (gender unknown) 1996–2004, returns 1997–2005.

	No. banded		No. returned		%	
Species	Adults	Nestlings	Adults	Nestlings	Adults	Nestlings
Sprague's Pipit	48	160	1	0	2.1	0.0
Savannah Sparrow	37	193	2	3	5.4	1.6
Grasshopper Sparrow	45	138	4	0	8.9	0.0
Baird's Sparrow	117	103	6	0	5.1	0.0
Totals	247	594	13	3	5.3	0.5

casionally captured off-site throughout Bowdoin NWR.

Male Sprague's Pipits were generally detected only during territorial displays that occurred 50–100 m above the ground (Robbins 1998). Thus, reobservation required either recapture or luring individual males within viewing distance using tape playback of conspecific song. We also were able to reobserve individual Sprague's Pipits in nests monitored with miniature video cameras (SLJ and PJG, unpubl. data).

We assumed no significant effect of capture, handling, or bands on return rates; to our knowledge, there were no capture-related injuries or mortality. Similar techniques did not negatively affect return rates of female Wood Thrushes (*Hylocichla mustelina*), including hatching-year birds (Perkins et al. 2004). Analysis of the use of colored bands (most of the same colors that were used here) on a migratory population of American Goldfinches (*Carduelis tristis*) showed that color bands did not appear to affect return rates (Watt 2001).

RESULTS

Return Rates.—Thirteen banded adult males were reobserved (5.3%, $n = 247$) (Table 1). Grasshopper Sparrows had the highest proportion of adult male returns (8.9%), followed by Savannah Sparrows (5.4%), Baird's Sparrows (5.1%), and Sprague's Pipits (2.1%) (Table 1). Ten of the 13 reobserved adult males were confirmed to have returned to the same site where they were originally captured. The remaining three (one each for Sprague's Pipit, and Grasshopper and Baird's sparrows) could not be identified to individual and we were unable to identify their sites of origin.

Capture Effort.—Our targeted mist-netting technique was effective in capturing territorial adult males of all target species. Using the number of nests located as an index to territory abundance, our capture ratio of adult males to number of known nests was less than one for Savannah Sparrows (0.24), Sprague's Pipits (0.62), and Grasshopper Sparrows (0.63). However, our capture ratio exceeded unity for Baird's Sparrows (2.6), which suggests that our sample may have included transients, as well as individuals whose nesting attempts had failed earlier in the season.

We banded Savannah Sparrow nestlings ($n = 193$) of which 1.6% were reobserved in subsequent years; no banded nestlings were re-sighted among the other target species ($n = 401$) (Table 1). Two of the reobserved Savannah Sparrow nestlings were identified to individual; one was observed at its natal site, and one was reobserved 4.8 km from its natal site. Ten female Savannah Sparrows were captured incidentally at the net. Among these, one adult female returned two consecutive years post-capture to the same site.

DISCUSSION

Three patterns of breeding-ground settling have been described for upland grassland waterfowl, characterized as homing, opportunistic, and flexible (Johnson and Grier 1988). Homing, where adults return to the same breeding area used before, is thought to be a response to relatively stable and ostensibly more predictable habitats. Opportunistic settling, where the individual settles in the first suitable site encountered in its breeding range, regardless of conditions in former breeding areas, is generally thought to be a response to less stable (less predictable) habitats. Flexible settling is where the individual will return to an area used previously, but moves elsewhere if that area has become unsuitable. Opportunistic or flexible settling would be expected to occur more frequently in endemic grassland birds than homing as an evolutionary response to habitat variability inherent in grasslands. Indeed, many grassland bird populations undergo considerable annual changes in distribution and abundance in the northern Great Plains (Johnson and Grier 1988, Shane 2000, Herkert et al. 2001, Green et al. 2002).

Annual return rates for all species reported here suggest low site fidelity. Reviews of studies of woodland and shrubland migratory passerines reported a mean return rate of ~ 46% for adults (Green 1992, Johnson and Geupel 1996, Gardali et al. 2000). Our study is consistent with a return rate of 5.3% (n = 95) reported for Baird's Sparrows in North Dakota (Green 1992). Moreover, it has been suggested that lack of geographic variation in bird songs (e.g., Baird's Sparrows) may also indicate an opportunistic settling pattern, since regional dialects would have difficulty forming in populations with substantial between year mixing (Kroodsma and Verner 1978, Green 1992, Kroodsma et al. 1999).

Our data are inconsistent with some reobservation data for Savannah and Grasshopper sparrows from other geographic regions of their respective breeding ranges (Bedard and LaPointe 1984, Wheelwright and Rising 1993, Vickery 1996). Multiple studies of Savannah Sparrows in eastern North America showed a mean return rate of 46.1% (SLJ, unpubl. data), primarily in grasslands but including salt marsh (Bedard and LaPointe 1984). Nestling Savannah Sparrows showed natal philopatry in New Brunswick island habitats (Wheelwright and Rising 1993). Grasshopper Sparrow return rates varied geographically, being lower in the Midwest and prairie regions than in the East, with return rates varying between 0 and 52% for migratory populations (Kaspari and O'Leary 1988; Vickery 1996; Balent and Norment 2003; B. K. Sandercock, pers. comm.). In Connecticut, 50% (n = 10) of those banded in 1986 returned in 1987; in Kennebunk, Maine, male return rate was estimated at 35% (n = 42) during a 3-year period; in California, 20% (n = 35) of the adult males returned (Vickery 1996). Return rates for Grasshopper Sparrows in the Midwest were lower with 19.8% (n = 111) adult males returning to Fort Riley in Kansas (B. K. Sandercock, pers. comm.), while no banded adults or juveniles (n = 85) were reobserved during a five-year study on Arapaho Prairie, a mixed-grass prairie in the Sandhills of Nebraska (Kaspari and O'Leary 1988).

Our relatively low reobservation rates suggest three possibilities: (1) low probability of reobservation of banded individuals, (2) low survivorship, and (3) low site-fidelity. Reobservation of adults on-site was straightforward and not problematic, although only limited time was spent searching adjoining areas for banded individuals. We were unable to calculate meaningful survivorship estimates using mark–recapture statistics since our return rates were too low (Murphy 1996). Therefore, either our survival was much lower than rates typically estimated for passerines, which seems unlikely, or our return rates were actually low and many of the adults that did not return moved to new breeding sites. Discounting low reobservation and survivorship, our results indicate a nomadic migratory pattern for our study species, suggesting opportunistic or flexible settling patterns, indicative of species adapted to historically unstable breeding habitats (Owens and Myers 1973, Andersson 1980, Johnson and Grier 1988). However, we cannot ignore the fact that some of our birds returned to our sites to breed; indeed, Green (1992) also found that a small number of Baird's Sparrows returned and bred in the same territories in subsequent years. This suggests that at least a small percentage of individuals of these species are site faithful while the rest settle with flexible or opportunistic patterns.

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SUET CARVING TO MAXIMIZE FORAGING EFFICIENCY BY COMMON RAVENS

CRAIG COMSTOCK[1]

ABSTRACT.—Most birds consume hard animal fat (suet) through repetitive pecking. Suet hardens considerably as the temperature declines below freezing. The caloric value of suet during the winter months is such that it is worthwhile for many birds to continue simple pecking as temperatures decline, but with diminishing returns. Some Common Ravens (*Corvus corax*) exhibit a more complex behavior while caching, or feeding young. I report an apparent territorial pair that repeatedly divided suet by carving deep grooves into it. Substantially larger portions of suet and other foods were isolated through this advantageous behavior and carried off, than would be possible through simple pecking. *Received 3 February 2006. Accepted 2 September 2006.*

Animal carcasses serve as important food sources for many animals during winter. Birds such as Black-capped Chickadees (*Poecile atricapilla*), White-breasted Nuthatches (*Sitta carolinensis*), Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), and Common Ravens (*Corvus corax*) commonly use their bills to peck at, and acquire, suet (hard animal fat). Suet becomes increasingly hardened as temperatures decline. Even so, most birds continue to acquire small particles of suet through simple pecking, although they are not easily carried away in large quantities.

Heinrich (1989) witnessed a wild raven (later joined by its mate) hacking off bits of meat from a frozen carcass and stacking them in a pile next to where it was working, something Heinrich had not seen before. The bird then filled its gular pouch with more meat from the carcass, picked up the pieces in the pile, and flew off. This was repeated eight times in the space of an hour. Subsequently, when several ravens were seen feeding at the same site, none was observed to stack meat they had torn off.

Heinrich (1999b) noted grooves in the suet where ravens had been feeding at a suet station in Vermont. The evidence suggested that ravens had sectioned and transported portions of suet, although he did not observe this behavior directly. I also have observed ravens foraging on suet and exhibiting both "Stacking" and "Carving" behavior as part of my study of a pair of ravens in Maine. It is possible these behaviors are more likely to occur in the absence of other ravens. I document the details of carving, herein.

During the early part of my study the question arose as to whether the isolation of a particular portion of suet was the focus of a unique behavior, or merely incidental to the acquisition of an immediate reward. It was possible that, using its heavy bill, a raven received a greater reward more easily by carving a groove, than by simple pecking. Perhaps the primary focus was packing the bill with suet particles, and isolation of substantial portions was a fortunate result.

METHODS

I attracted a pair of wild ravens (1996–2005) to the wooded area of my property in Starks, Somerset County, in western Maine. Initially, I provided them with whole, and partial carcasses of road-killed native mammals, on an occasional basis (<1/month) and at varying locations within the 28 ha. Beginning 17 September 1997, a remote video recorder (a modified consumer camcorder) monitored each of the feeding locations in turn. No more than two adult ravens were observed at any one time from that date until the conclusion of the study in May 2005. The pair was neither marked nor was gender genetically ascertained.

I hoped to study the pair without interference from other ravens and took steps to make the study site less attractive to increase the likelihood the presence of any vagrants or replacements would be noticeable. I offered smaller quantities of food (<500 g), in a secluded conifer stand that became the permanent study site during 1997–2005. The pair was encouraged, gradually, to take meat

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scraps from beneath a small (850 ml) plastic container. The container was placed on its side initially, with scraps near and within it. When the pair hesitantly began taking scraps from the container daily I inverted it, and in this manner concealed all food subsequently offered at the site throughout the study. Food was not offered elsewhere on the property. Ravens are neophobic (Heinrich 1988). Both ravens were exceedingly apprehensive for nearly three months, displaying bill-clacking with the head tipped back, sideways crouching, and multiple jumps or flying off when approaching the container. It is likely that a vagrant or a replacement to one of the pair would require an adjustment period as well, and their presence would be evident on the daily videos.

A camouflaged video camera was gradually moved to within 2 m of the study site to monitor behavior closely beginning on 9 November 1998. A second camera was added later for alternate views. I ran two cables from the site to my study, allowing me to watch activity on separate monitors, and to record the video from either of the two cameras in VHS and digital format. Digital recordings allowed a frame-by-frame analysis of the ravens' behavior in addition to providing a permanent log of activity. Camera #1 offered a close-up image. Camera #2, at right angles to it, offered the choice of an additional close-up, or a wider angle with which to view a portion of the ravens' most commonly used flight path and occasional nearby cache sites.

A raven nest site was located 1 km to the west by noting the pair's flight paths along a town road and near open fields during the 1999 nesting season. Subsequent nesting (2000–2005), took place within 500 m of the 1999 site. Juveniles (2–5) calling and begging appeared each May and June (1999–2005) in company of one or two adults. The ravens were rarely fed during July and August to discourage juveniles from returning. Open fields 300 m to the west and positions along a paved town road running directly towards the nesting area from our property afforded good views of some caching, and flights to feed young. I installed an audio transmitter near the cameras allowing me to monitor activity there with an audio receiver while I hid near the nest and observed the ravens' departures and arrivals. There was no audio or video evidence of activity at the study site when both ravens were in the vicinity of the nest. If one raven was seen at the nest, there was no more than one at the study site. A departure from the study site was followed in a minimum of 4 min by an arrival at the nest.

I offered suet, partly buried in snow, during winters 1999–2005. The plastic container was again inverted over the exposed portion to discourage scavengers and other ravens. I measured food offered to examine the pair's volume and weight carrying capabilities. To measure volume, I cut raw poultry into 10 mm cubes to ensure they would fit easily within the bill and gular pouch. I also offered large pieces of suet, to measure their upper limits of weight-carrying capacity. Up to 2 kg of food was offered at a time, but the amount offered averaged 100–200 g, sufficient to attract the pair daily but discouraging their dependence on the supply. Daily feeding was discontinued upon completion of the study.

Visual Cues.—Protrusions, and variations in texture and color over the surface of natural suet appeared likely to influence where carving would commence. Natural layers often affected where separation would occur. It was impossible to identify whether the raven chose a point on the suet's surface to begin carving, or was drawn to it as a result of visual cues. The isolation of large portions of natural suet could be accidental. Thus, purified suet was cast into 6 individual cylinders and offered, beginning in winter 2001, to eliminate the effects of such variables and to quantify those portions separated by each raven. White in appearance, the pure suet cylinders bore no texture or color variations. The cylinders were offered occasionally, one at a time. Subsequently, 7 cylinders cast of a mixture of suet and ground beef, a composition more difficult to carve, were also offered one at a time. All cylinders were 30 or 60 mm in diameter and varied in length from 18 to 60 cm. Both ravens were present when 5 of the cylinders (4 suet, 1 beef-suet) were divided. Knowledge of their size and weight allowed for drawings approximating the actual portions removed by each raven.

RESULTS

Apparent Bill/Gular Carrying Capacity.—The approximate volumes the ravens could be

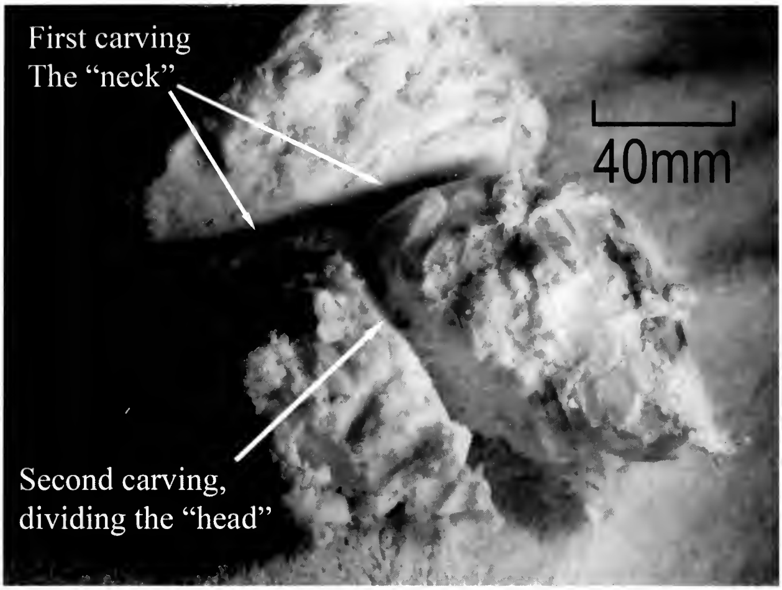

FIG. 1. Suet, secured in place by ice, carved by a male Common Raven in Starks, Somerset County, western Maine, during January 2001. The male raven could not complete the carved "neck" and resorted to dividing the "head" into two pieces. Each piece was subsequently removed through additional carving.

expected to carry as a result of simple pecking were ~50–55 cc, based on volumetric measurements of the poultry cubes provisioned. This is comparable to ~46.5–51 g of suet (at ~0.93 g/cc). Both birds made extended flights (>500 m) while carrying suet pieces weighing ~350–400 g. Occasionally heavier loads (<500 g) were cached at distances of <100 m.

Carving Behavior.—When simply pecking, the raven drives its closed or slightly open bill against the suet. If subsequent pecks are continued in line with the first, a shallow groove begins to form. Carving is the extension and deepening of such grooves. Carving occurred most commonly at temperatures of −15° C or lower. At higher temperatures, suet was broken easily by the raven's heavy bill. Both birds carved, directing their bills in line with the groove, and only rarely at right angles to it.

If the portion of suet being carved was sufficiently thick, the ends of the groove were extended until they began to encircle, and form a "neck" (Fig. 1). One raven often repositioned the suet or rolled it over completely, to continue. In each of more than 50 instances of encirclement carving observed, the extended ends of the groove were joined on the opposite side. The "neck" thus created, was then deepened until the portion was separated. I observed carving behavior on more than 100 occasions considering all natural suet and the cast cylinders offered.

Immediate Rewards.—During the course of carving, suet "shavings" collected in the ravens' bills. Some of these were swallowed, as both birds fed occasionally while carving. However, many shavings were not consumed and one bird often paused while carving to expel wads of suet shavings, placing them to one side on the snow. Once carving was complete, the deposited wads were gathered, the recently separated piece(s) of suet were taken up, and the flight to the nest or cache site was made.

Behavioral Differences.—The gender of each raven was not definitively determined but there were notable differences in the behavior of the two birds. The apparent male was consistently observed to take more and larger suet portions than the apparent female. He dominated the suet whenever the two were together. While carving, the apparent male sometimes "growled", and occasionally struck at the female if she approached within

~30–40 cm. The apparent male was present at the site, daily, throughout each of the nesting seasons. The apparent female, the more cautious and slightly smaller of the two, was absent from the site during the early part of each nesting season (1998–2005). The apparent female normally waited until the male departed before approaching the suet, then broke off small pieces and took scraps the male had left behind. Of the 13 suet cylinders offered, 8 cylinders were divided by the apparent male alone. One of these was offered at the site on 05 February 2002, the remaining 7 were offered between 12 March 2002 and 10 April 2002. The apparent female did not appear at the site on those dates.

Of the 5 cylinders divided while both ravens were present, the apparent female participated in the division of only 2, isolating a total of 16 portions of suet averaging ~17 g each. Her flight load average was less than half the calculated upper limit for simple pecking. Additionally, she flew off with portions the male isolated; one each from 4 of the 5 cylinders, averaging ~177 g. The largest single portion she carved alone was ~115 g.

The apparent male isolated 21 portions from the 5 cylinders, averaging ~156 g each. Of the 8 cylinders he divided alone primarily through carving, the male isolated 33 portions averaging ~147 g each. His average flight load while carving all cylinders was ~150 g—nearly three times the calculated limit for simple pecking. Thirty percent of his flight loads were four times the limit. His largest single portion from the cylinders was ~418 g.

DISCUSSION

Flight loads that clearly approached the upper limits of the raven's carrying ability in size or weight were considered maximized for the purposes of this study. Attempts to increase or maximize flight loads were a notable aspect of the behavior of the apparent male. This was particularly true during the eight nesting seasons documented (1998–2005). Ravens have exhibited similar behavior at widely separated geographical locations when offered non-natural foods such as doughnuts and crackers (Heinrich 1989).

The products of carving are small immediate rewards, short-term rewards, and larger (in number or size) long-term rewards. With simple pecking, the immediate reward for striking with the bill is the acquisition of a small portion of suet. Repeated blows to the suet yield additional immediate rewards—incentives to repeat the action. A full bill, to a raven, represents a short-term reward, the sum of a series of immediate rewards. On more than 200 occasions, the pair was observed to forego consumption or transportation of both immediate and short-term rewards (wads and other substantial pieces), while continuing to isolate additional suet through carving. Wads were placed aside when the quantity within the bill interfered with carving, evidence that a full bill was not sufficient incentive to discontinue the carving process.

There were no noticeable differences in the carving of the pure suet and ground beef-suet cylinders. The division of the cylinders offered made it clear that visual cues and layers in natural suet could, but did not necessarily affect the size of isolated portions. The two-dimensional drawings made from videos did not allow for precise measurements but the differences between quantities the apparent female and male isolated were adequately represented for the purposes of this study. The average portions carved by the apparent male in both natural and cast suet represent substantially greater volumes than he could have acquired through simple pecking. This is particularly apparent when compared to the averages for the apparent female under similar circumstances. Additionally, the cylinders offered a consistency in their shape and composition that natural suet does not provide. While anecdotal, on 28 March 2002, the male carved a 30 mm × 60 cm cylinder into 6 individual portions averaging ~64 g, before departing with any of them. Substantial portions of both natural and cast suet carved by the apparent male while placing wads and other small portions aside, cannot be described as incidental to the acquisition of an immediate reward. The evidence strongly suggests that maximizing flight loads was the focus of his behavior, and that carving was an efficient means to that end.

Ravens in New England begin building nests in mid-February. The 4–7 eggs are incubated by the female for 21 days. The young are then continually brooded by the female while they are still unable to regulate their body temperature and grow rapidly on the food the male provides (Heinrich 1999a). While the apparent female studied was slightly smaller than the male, evidence suggests the differences in the amount of carving may represent long-term patterns of behavior, rather than differences in ability. If this is typical for territorial pairs, less carving by the female and her smaller average flight loads may represent behavior developed to conserve body mass for the cold nesting season. This would also allow the male to demonstrate his effectiveness as a provider—a critical component of a pair's success in raising young.

The extent to which carving may be practiced by other ravens is not yet known. I offered natural suet daily over the course of a 2-week period to another pair at a distant location, and did observe occasional carving behavior. That, and Heinrich's observation of one of a pair of ravens cutting, and piling chunks of meat at a carcass in the absence of other ravens, similar to behavior that I have witnessed in Starks, Maine, suggests these behaviors may be more common than previously believed, but less likely to occur when other ravens are present.

ACKNOWLEDGMENTS

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Short Communications

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Corvids in Combat: With a Weapon?

Russell P. Balda[1]

ABSTRACT.—I report on an incident involving a Steller's Jay (*Cyanocitta stelleri*) and an American Crow (*Corvus brachyrhynchos*) at a feeding platform. After repeated failures to drive the crow from the platform by scolding, approaching and diving at it, the jay flew into a bush where it worked vigorously to break off a stick. Having broken off the twig, the jay, with stick in bill, approached the crow and thrust the pointed stick at it. The crow lunged at the jay which then dropped the stick. The crow picked up the stick and flew after the jay. This appears to be the first case of a bird holding an object and using it in a weapon-like way during an aggressive action against another bird. *Received 19 October 2005. Accepted 27 July 2006.*

On 26 April 2004 at 0655 hrs MST I observed the following interaction at a bird feeding station in Flagstaff, Arizona at 2,000 m elevation. The feeding platform measured 1 × 1 m and was within 2.3 m of the window through which the observations were made. The roof overhang was 2.2 m. from the center of the platform and 2.7 m above it.

OBSERVATIONS

A solitary American Crow (*Corvus brachyrhynchos*) was on the platform eating seeds. A pair of Steller's Jays (*Cyanocitta stelleri*) flew into a mountain mahogany (*Cercocarpus montanus*) shrub that borders the platform. The platform was stocked daily with a variety of seeds commonly eaten by local birds. Steller's Jays regularly feed at the platform, eating and carrying sunflower seeds off to cache. Crows only occasionally visit the platform and are selective about which seeds they pick up in their bills. Thus, they feed deliberately and slowly, and spend considerable time on the platform.

One of the Steller's Jays flew to the edge of the platform and scolded loudly while facing the crow for about 10 sec. The crow paid no heed to the scolding jay as it continued feeding. The jay on the platform then made feinting movements toward the crow with its bill extended in the direction of the crow. The jay cautiously and haltingly approached the crow as if to attempt to pull its tail or peck it. The jay approached to within 7–10 cm of the crow and appeared to be in the throes of a "fight or flight" conflict. The crow then turned to face the jay and hopped in its direction. The jay quickly hopped backwards. The jay again approached the crow making jabbing motions toward it as it continued to scold loudly. Each time the jay approached, the crow turned to face it and make a slight lunging movement toward it. This exchange was performed six times. The jay then flew to the roof of the house directly above the crow and scolded loudly for 5–6 sec. The crow continued to pick seeds from the platform. The jay then swooped down toward the crow just missing its head and back. The crow jumped at the jay but no bodily contact occurred. The jay again flew onto the roof and called loudly for 5–6 sec. The jay then dived a second time at the crow, again narrowly missing its head and back. The crow continued to feed from the platform.

The jay then flew into the mountain mahogany and vigorously worked with its bill to break off a twig from a dead branch. The jay succeeded in breaking the twig from the branch and held it in its bill so that it pointed forward. The twig was about 10 cm in length, and about 0.75 cm in diameter. The twig end in the jay's bill was rather blunt; in contrast, the other end was pointed. The jay then flew to the feeding platform with the twig in its bill. The jay lunged at the crow with the pointed end of the twig directed at the body of the crow. The stick missed the crow by only a few cm. As the jay approached, the crow lunged quickly at it. The jay flew up with a startled jump backwards, wings extended, and again

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landed on the platform and dropped the twig onto the platform. The crow then picked up the twig in its bill and lunged at the jay with the stick pointed at the jay. The two jays then flew off and the crow followed them with the twig in its bill.

Was the twig a weapon? If so, do we define a weapon as a tool? In animal behavior, usual definitions of a tool indicate that tools must be extensions of the body of the organism that are used in a way that allows the organism to exploit a resource or situation that could not be exploited without the object used as a tool. Also, in the case of birds, the tool must be an extension of the bill or feet. In the usual sense, the meaning of "extension of the bill" would refer to a feeding apparatus, but bills are also used by birds in aggressive interactions. Thus, even in the strictest sense this case appears to be one of tool use. The twig was a tool that was used as a spear or a lance to be thrust at a potential enemy as an extension of the bill. The purpose for using the twig as a weapon was, ostensibly, to drive the crow from the feeding platform, something the jay had failed to do by scolding, approaching aggressively, and aerial attack. The jay may have viewed the crow as a food competitor or as an impediment blocking its access to the feeder. Whether or not it was the jay's intention to use the twig as a weapon when it returned to the feeding platform with it, the twig appeared to take on this function. The crow's intentional use of the twig as a weapon is more problematic given that it had previously "lunged" at the jay without a tool. An alternate explanation might be that the crow picked up the twig out of curiosity and then lunged at the jay because it was close by.

The jay broke the twig off the shrub. The twig was of such a length and width that it could be easily manipulated by the jay. This behavior can be cautiously interpreted as weapon construction. Having failed to drive the crow from the platform using three other methods, the jay used a twig as a lance against the crow. Possibly, the crow then proceeded to use this newly acquired weapon against the jay. In this scenario both species were using a tool against each other, first the jay against the crow and then the crow against the jay.

DISCUSSION

Tool use by birds has received considerable recent attention (Lefebvre et al. 2002; Emory and Clayton 2004a, 2004b). These authors conclude that tool use by birds is more common than previously thought. Lefebvre et al. (2002) recently catalogued all reported cases of tool use by all birds that were published in 68 short note sections of journals as well as previous reviews. They found 39 "true" use of tools (objects detached from the substrate and held in foot or mouth, McFarland 1982) and 86 "borderline" cases (defined as objects that are of the substrate such as anvils, wedges, thorns, and bait) (Hansell 1987, Vauclair 1997). The Common Crow used the most techniques (n = 5) with other members of the Corvidae also possessing an impressive repertoire of tool uses. For example, Blue Jays (*Cyanocitta cristata*), close relatives of Steller's Jays, were observed tearing paper and using it to rake in food from outside their cages (Jones and Kamil 1973). The New Caledonian Crow (*Corvus moneduloides*) may use the most complex tool construction and use behavior of any known bird. They have been observed constructing tools of different types to solve different types of foraging challenges. Useful tools are then carried around during foraging bouts (Hunt 1996; Chappell and Kacelnik 2002, 2004).

Tool use by corvids should not be that surprising given their large brain (Marzluff and Angell 2005) and considerable cognitive abilities (Emery and Clayton 2004a, 2004b; Emery 2006). Lafebvre et al. (2002) found a positive correlation between true tool use and brain size. Tools used as weapons, however, seem less common in birds. Corvids have been known to drop objects on humans that are threatening nests or offspring (Caffrey 2001), and Boswell (1983) cites a case of a Black Eagle (*Aquila verreauxii*) dropping sticks on nest intruders.

Behaviors that are classically associated with lance or spear use were observed in this bout. The jay first *selected* and *prepared* an object that could readily be used as a spear, and then *lunged* at the crow with the spear, the crow startled the jay which then dropped the twig. The crow retrieved the twig and possibly used it against *the* jay. The current report may be the first incident of a bird holding an object and using it in a weapon-like fashion during an aggressive action against another bird. The incident reported herein adds to our understanding of how a variety of items in a bird's environment may be used to aid in pursuit of resources and to gain control over their living space.

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Turkey Vultures Use Anthropogenic Thermals to Extend Their Daily Activity Period

James T. Mandel[1,3] and Keith L. Bildstein[2]

ABSTRACT.—We describe predictable nocturnal soaring flight in Turkey Vultures (*Cathartes aura*) feeding at a landfill in eastern Pennsylvania. Birds feeding at the landfill returned to their roosts each evening by gaining altitude while soaring in thermals above flared methane vents at the site. Our results highlight behavioral plasticity in this species, which, in part, may explain why Turkey Vultures are so common throughout much of their extensive range. *Received 5 December 2005. Accepted 3 May 2006.*

Turkey Vultures (*Cathartes aura*) are energy minimizers like most avian scavengers (*sensu* Schoener 1971, Ruxton and Houston 2002). Individuals at rest maintain low metabolic rates for their body mass and reduce their core body temperature at night in apparent efforts to conserve energy (Heath 1962, Wasser 1986). Turkey Vultures in flight usually soar and glide when flying between roosts and previously located food, when searching

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for new sources of food, and during migration (Pennycuick 1972, Mundy et al. 1992, Kirk and Mossman 1998, Ferland-Raymond et al. 2005). At times, the species engages in intermittent flapping flight, particularly when departing from and descending into their roosts. This behavior is generally rare except when updrafts are unpredictable or weak. Our observations, assisted by radio tracking, indicate that lack of sufficient assisted lift can ground individuals several days or more (JTM, pers. obs.). Turkey Vultures have long been known as "late risers" (Ludlow Griscom *in* Bent 1937) that usually restrict their daily activities to mid morning to late afternoon when thermal- and slope-soaring are possible (Kirk and Mossman 1998).

Anecdotal and possibly disturbance-induced nocturnal flight has been reported in the species (Tabor and McAllister 1988) but regular nocturnal flight is unknown. Here, we report regular nocturnal flight in Turkey Vultures returning to their roosts in the evening after soaring in anthropogenic thermals created by flared methane at a landfill in eastern Pennsylvania.

METHODS

We watched Turkey Vultures on 120 nonrainy days from 12 July to 5 November 2004, and from 20 June to 17 July 2005, at a 45-ha Waste Management, Inc. landfill in Pen Argyl, Northampton County, Pennsylvania (40° 52′ N, 75° 15′ W). Birds were observed continually from 0730 to 2315 hrs EST, with a 3-hr break from 1300 to 1600 hrs EST. Observations were from an unused hilltop on landfill property, with the farthest roost being ~300 m. Adequate artificial lighting at the site permitted nocturnal observation without special equipment. Prior to the observations detailed here, we observed vultures at three communal roosts near the landfill for 20 days in June 2004 and for 47 days in July and August 2003. Our roost-site observations, which were conducted from dawn until dusk, and included both unmarked individuals and radio-marked birds, are used here to establish a temporal baseline for vulture behavior in the area.

Methane is vented at two sites at the landfill. One site, the "big flare," consists of a group of three 10-m-high vent pipes. The other site, the "little flare," consists of a single 10-m vent pipe. At both sites methane is flared continuously, around-the-clock, 365 days a year.

OBSERVATIONS

Between 30 and 90 Turkey Vultures fed at the landfill daily. On more than 70% of the days, 10 to 15 individuals fed until 2100 to 2300 hrs EST or approximately 90 to 210 min after local sunset. We do not know whether the late-feeding birds were the same individuals each day, or whether a larger subset of the population engaged in late feeding on an occasional basis. Vultures that fed in farmlands, woodlands, and suburban areas near the landfill returned to their roosts before 2000 hrs EST or, at most, 30 min after the local sunset.

Turkey Vultures that left the landfill used both natural thermals and anthropogenic thermals at the methane vents throughout the day to gain lift before departing the site. When natural thermals were no longer available after sunset, vultures that left the landfill initially approached the vents in flapping flight, and then circle-soared to approximately 100–200 m in thermals above the vents before gliding in the direction of nearby roosts. On most days, 10 to 30 vultures arrived at the landfill before 0800 hrs EST, soared above the vents for several minutes, and then departed, presumably for more distant feeding sites.

Turkey Vultures feeding at the site roosted in three communal roosts within 4 km of the landfill. Two of the roosts contained 30–50 Turkey Vultures and 5–10 Black Vultures (*Coragyps atratus*). A third roost contained 10–15 Turkey Vultures. Black Vultures at times fed at the landfill but none remained as late in the day as Turkey Vultures, and none soared in thermals above the vents.

DISCUSSION

Thermals created by flared methane appeared to be considerably stronger and hotter than nearby "natural" thermals. Vultures soaring above the vents ascended more rapidly than those soaring in nearby natural thermals, and many appeared to have difficulty maintaining level flight while doing so. Most of the birds that flew within vent thermals did so intermittently, and rather than circle-soaring radially about the center of the thermal while ascending constantly, circle-soared tan-

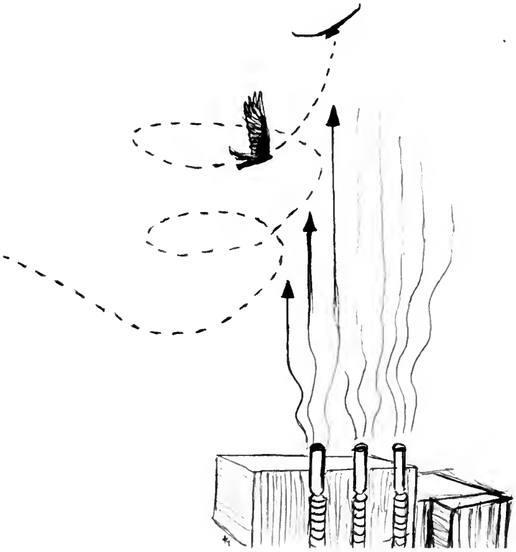

FIG. 1. The "big flare," the main methane vent facility at the Waste Management, Inc. landfill in Pen Argyl, Pennsylvania. Vultures soaring with the thermal created by the flared methane at the vents do so tangentially, rather than radially.

gentially within the thermal for brief periods and then circle-glided outside the thermal for longer periods (Fig. 1). We believe that individuals did so because they were not able to soar continually within the vents. Workers at the site reported finding Turkey Vulture carcasses at and near the bases of the vents, suggesting that in addition to providing soaring opportunities for vultures, the anthropogenic thermals at the vents also killed them, most likely either by scorching or suffocating individuals. Thus, the vents may have created an "ecological trap" for the birds that used them (Schlaepfer et al. 2002).

That Turkey Vultures, but not Black Vultures, soar in vent thermals at this site may be due several factors. First, many vultures that roosted nearby searched for carrion in the surrounding landscape rather than for food refuse at the landfill, suggesting that food was limited at the landfill. We tested this hypothesis by placing a road-killed white-tailed deer (*Odocoileus virginianus*), a road-killed common raccoon (*Procyon lotor*), and a butchered chicken (*Gallus domesticus*) at visible locations at the site to examine the extent of competition for food. Up to six Black and Turkey vultures fed upon the chicken simultaneously, and up to 14 individuals fed simultaneously upon the deer. Black Vultures dominated Turkey Vultures at feeding sites, suggesting the former may be able consume sufficient food without prolonging the length of their feeding day. Second, Turkey Vultures typically hold their wings in a pronounced dihedral when flying low over the landscape, a self-righting aerodynamic "design" that stabilizes their flight in turbulent air (Mueller 1972), whereas Black Vultures do not. The relatively turbulent nature of thermals above the vents may have precluded their use by Black Vultures.

That Turkey Vultures are able to lengthen their daily activity periods via use of anthropogenic thermals suggests considerable behavioral flexibility in the species. This may help explain its large range and relative abundance.

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Mallards Feeding on Salmon Carcasses in Alaska

Jeffrey S. Gleason[1]

ABSTRACT.—Mallards (*Anas platyrhynchos*) are known to frequent rivers and streams during post-breeding. I describe observations of Mallards feeding on fresh Pacific salmon (*Onchorhynchus* spp.) carcasses in Alaska on two separate occasions during July–August 2005. These observations represent the first reported use of salmon carcasses by Mallards in Alaska. This strategy may be fairly common for a segment of post-breeding and fall staging Pacific Flyway Mallards in Alaska, particularly those that inhabit streams and rivers used by the five species of Pacific salmon during the spawning season. *Received 19 December 2005. Accepted 29 July 2006.*

The Mallard (*Anas platyrhynchos*), a ubiquitous dabbling duck distributed across North America, is a generalist omnivore. Diets of dabbling ducks vary geographically and seasonally, with animal (primarily invertebrates) and plant matter (natural wetland plants and agricultural crops) comprising the bulk of diets in spring/summer and fall/winter (Bellrose 1980, Baldassarre and Bolen 1994). Importance of salmon (*Onchorhynchus* spp.) as nutrients to aquatic and terrestrial habitats is well documented (Cederholm et al. 1999, Hilderbrand et al. 1999, Gende et al. 2002, Reimchen et al. 2003, Gende et al. 2004, Hilderbrand et al. 2004). This has led some researchers to consider that salmon are keystone species (Willson and Halupka 1995). A wide variety of vertebrates, including birds and mammals, consume anadromous salmon as predators of live fish or as scavengers of carcasses. A diverse assemblage of birds (including the Mallard) has been identified as consuming salmon eggs or juvenile offspring (i.e., alevin or parr) (Cederholm et al. 1989, table 7; Willson and Halupka 1995, table 1). In this paper, I report the consumption of salmon muscle tissue and internal organs by Mallards.

OBSERVATIONS

On 16 July 2005 while fishing on the Kenai River near Soldotna, Alaska (150° 58′ W, 60° 28′ N), I observed (1100 hrs AST) an adult female Mallard and five ducklings (Class III, Gollop and Marshall 1954) tipping-up and removing flesh from sockeye salmon (*Onchorhynchus nerka*) carcasses discarded after being filleted by anglers. The female with her brood proceeded upstream between the anglers and the riverbank, periodically tipping-up to dabble on carcasses. I witnessed 4–5 separate feeding attempts over ~15 min before the female and brood left my field of view.

On 13 August 2005 while fishing at Sheep Creek Slough near Willow, Alaska (150° 05′ W, 61° 58′ N), I observed (1000 hrs AST) a single adult male Mallard feeding on coho salmon (*Onchorhynchus kisutch*). The Mallard was surface dabbling and feeding with neck submerged. I observed the Mallard ingest a sperm sac and several relatively small fragments of muscle tissue carried downstream from a fish cleaning station. During observations at both locations, I was sufficiently close (<3 m) to the Mallards to observe ingested items pass the esophagus.

DISCUSSION

Mallards have been known to feed on perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), dace (*Leusciscus vulgaris*), and three-spine stickle-

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backs (*Gasterosteus aculeatus*) in Europe (Harrison and Harrison 1962, Vinicombe 1979, Harris 2005). Mallards have also been documented feeding almost exclusively on rainbow smelt (*Osmerus mordax*) during winter in North Dakota (Olsen and Cox 2003). Mallards wintering below the Garrison Dam in North Dakota fed by dabbling on entrained rainbow smelt that had passed through the dam (R. R. Cox, unpubl. data). The use of salmon eggs by Mallards in Alaska is apparently a common foraging strategy (T. C. Rothe, pers. comm.). Sizeable concentrations of Mallards were observed at creek mouths littered with chum (*Onchorhynchus keta*) and sockeye salmon carcasses (P. L. Flint, pers. comm.) during September aerial surveys at Izembek Lagoon. It could not be ascertained from the aircraft if Mallards were actually feeding on salmon carcasses, salmon eggs or invertebrates attracted to the carcasses. Alternatively, these flocks of Mallards may have been using these areas simply due to freshwater. Esophagi from Mallards harvested subsequent to these surveys from an inland freshwater lake, approximately 1.6 km from the creek mouths were "full" of salmon eggs (P. L. Flint, pers. comm.). The lake is <1 km from several known spawning sites. My observations in conjunction with those of others in Alaska suggest that some post-breeding and staging Mallards in Alaska may incorporate salmon flesh and eggs as a regular part of their diets. Salmon may also be relatively important to staging or wintering Mallards elsewhere in the Pacific Northwest (Munro 1936, 1943; Kortright 1943). Mallard food habits and foraging behavior are plastic, allowing individuals of this species to capitalize on locally abundant, high energy food sources. It is not known to what extent Alaskan breeding Mallards rely on salmon-derived nutrients as part of their seasonal energy budget. I hypothesize that post-breeding (both ducklings and flightless adults) and fall staging Mallards in Alaska opportunistically use or actively select salmon carcasses (and eggs) as a readily available and predictable high energy food source (i.e., protein or fat).

ACKNOWLEDGMENTS

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Effects of Dummy Global Location Sensors on Foraging Behavior of Cook's Petrel (*Pterodroma cookii*)

Matt J. Rayner[1]

ABSTRACT.—The effect of 4.5-g dummy geolocation loggers on the foraging ability of Cook's Petrel (*Pterodroma cookii*) was assessed over single foraging trips from Little Barrier Island, New Zealand. I compared foraging trip duration and chick provisioning between equipped and unequipped birds and could not detect a detrimental effect of loggers on either parameter. The lack of effect of these loggers may be the result of their small size, the short-term nature of their use, and foraging strategies used by Cook's Petrel. Geolocation studies involving Cook's Petrel and other small gadfly petrel species may be feasible for single foraging trips. *Received 1 May 2006. Accepted 28 August 2006.*

Remote telemetry studies provide an increasingly widening window into the study of petrels (Procellariiformes) (Fernandez et al. 2001, Phillips et al. 2006). A range of studies has shown this technology can have adverse effects upon tracked individuals. Thus, awareness of the impacts of tracking equipment is crucial prior to the commencement of work with any petrel species and other study subjects (Söhle et al. 2000, Phillips et al. 2003, Igual et al. 2005). The size of available technology has limited at-sea studies to larger albatrosses and medium-sized procellarids (Brooke 2004). A new generation of lightweight Global Location Sensors (GLS loggers) (Afanasyev 2004) now presents opportunities for study of the movements of much smaller species (<400 g) across a broad range of taxa. There is currently no published work detailing the effect of GLS loggers on the foraging behavior of small petrels (<400 g).

METHODS

I examined the effect of dummy GLS loggers (DLs) on Cook's Petrel (*Pterodroma cookii*) over the course of single foraging trips from a colony on Little Barrier Island, New Zealand (36° 12′ S, 175° 05′ E). Twenty adult Cook's Petrels were captured (average adult weight = 200 g) (Imber et al. 2003) during 1–16 February 2006 from 10 burrows where they were returning to provision chicks. All adults were banded and DLs (20 × 15 × 6 mm, mass 4.5 g: <2.5% of adult body weight) attached to feathers between the wings of five randomly selected birds (L+) using tesa-tape (Tesa-Brand® 4124, Beiersdorf, Germany) following Söhle et al. (2000). Fifteen birds were used as controls (C) and handled for approximately the same duration as L+ birds. Birds were returned to their burrows and allowed to leave for sea of their own accord. Chicks were weighed daily at midday during the 2 weeks of the study to the nearest 2 g (using a 600 g pesola scale) to establish mean weight loss over a 24-hr period and allow for calculation of provisioning size. Returning adults were recaptured at night (one field worker each monitored 5 burrows) when exiting the burrow after feeding their chick and DLs were removed

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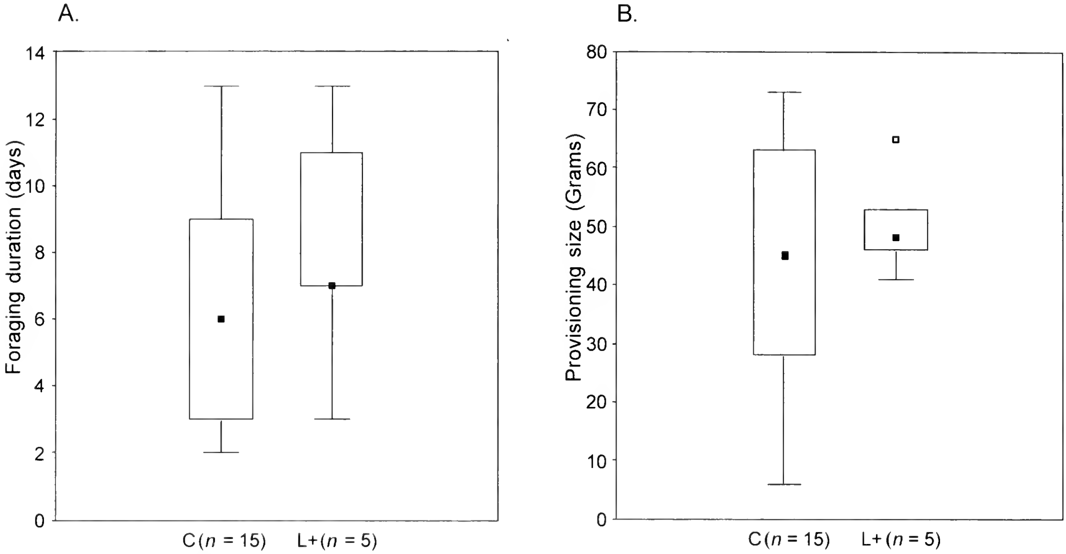

FIG. 1. (A) Foraging duration, and (B) size of provisioning provided to chicks for control (C) and logger attached (L+) adult Cook's Petrels tracked for single foraging trips. Black squares indicate median values, boxes represent interquartile ranges, bars represent minimum and maximum values, and empty squares indicate outliers.

from L+ birds. Each chick was weighed after the return of adults. The amount of food provided at each provisioning event was calculated upon completion of the study by adding half of the mean 24-hr weight loss to the post-provisioning weight increase (provisioning events occurred between 2200 and 0200 hrs).

RESULTS

All L+ and C birds were recaptured at the colony and four of five of the L+ birds returned with the DL still attached. Duration of individual foraging trips was highly variable ranging from 2 to 13 days in C birds and 3–13 days for L+ birds (Fig. 1A). L+ birds had a slightly longer mean (±1 SE) foraging duration (8.1 ± 3.4 days) than C birds (6.5 ± 3.3 days) but this difference was not significant (Mann-Whitney *U* test, $U = 25.5$, $P = 0.29$). However, the sample size statistical power, calculated using 2 sample *t*-tests, was low (0.29 @ $\alpha = 0.05$). The mean 24 hr weight loss for chicks over the 2 weeks of the study was 17.2 ± 1.9 g. Individual provisioning provided to chicks ranged from 6 to 74 g in C birds and 41 to 65 g in L+ birds (Fig. 1B). Mean provisioning size, was slightly greater for L+ birds (50.6 ± 4.5 g) than C birds (42.6 ± 18.0 g) but did not differ between treatments (Mann-Whitney *U* test, $U = 30.0$, $P = 0.55$) (power 0.20 @ $\alpha = 0.05$). No adults abandoned feeding their chicks as a result of this study and all 10 chicks fledged successfully at the end of March 2006.

DISCUSSION

Previous studies demonstrated a range of effects that reduced flight efficiency may have upon breeding petrels (>600 g) including (1) extension of foraging trips, (2) reduction in chick provision size, and (3) nest desertion (Mauck and Grubb 1995, Klomp and Schultz 2000, Freeman et al. 2001, Phillips et al. 2003). My preliminary results suggest little detriment of a 4.5-g attachment on foraging duration, chick provisioning, and fledging success for Cook's Petrel over single foraging trips. DLs returned exhibited no evidence that birds had attempted to remove the devices and the loss of one DL was attributed to attaching the device during wet weather when moisture may have reduced initial tape adhesion. Sample size and, thus, statistical power were low in this study. The lack of any demonstrable effect of the dummy loggers on Cook's Petrel is likely related to the size of the attachments, short-term nature of their use, and foraging strategies used by this species. Studies on petrels have demonstrated that attachment size is a key consideration, with devices greater than 3% of body weight being shown to negatively impact foraging behavior (Mauck and Grubb 1995, Freeman et al. 2001, Phillips et al. 2003). The DLs used were less than 2.5% of adult body mass, approximately 5% of the mean meal size carried by adults, and were used for single foraging trips. In addition, Cook's Petrels are gadfly petrels, a group of small to medium sized petrels that are primarily surface feeders (Imber 1985, Brooke 2004). Thus, birds would not be strongly affected by the underwater buoyancy or drag from an attached DL when feeding, unlike other small petrel taxa such as shearwaters (*Puffinus* spp.) and diving petrels (*Pelecanoides* spp.) that regularly make deep dives in pursuit of prey (Brooke 2004).

It is unlikely the energetic cost of carrying the DLs would have been absorbed by adult Cook's Petrels in this study to maintain frequency and duration of chick provisioning. Cook's Petrels are long-lived, trans-equatorial migrants and, like other petrels, an extremely K-selected species (Phillips et al. 2006). Their life-history strategy balances the breeding season requirements of chick rearing with need to minimize costs of any breeding attempt and extend fecundity over a long life span (Warham 1990, Brooke 2004). This strategy is dependent upon flight efficiency as birds must locate and exploit ephemeral prey sources over vast distances. Studies with petrels indicate that increases in foraging costs from experimental attachments are transferred to chicks rather than absorbed by adults (Mauck and Grubb 1995, Weimerskirch et al. 2000). Thus, any debilitating effect from an attached logger would be reflected in an extension of trip duration and/or reduction in chick provisioning. How attachment of GLS devices may affect adult petrels during more extensive periods of attachment and how other small petrel species may respond to these loggers remains unknown. Further studies should be conducted on petrel taxa exhibiting different foraging techniques to those of the Cook's Petrel.

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Eastern Screech-owl Hatches Wood Duck Eggs

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ABSTRACT.—I describe an Eastern Screech-owl (*Megascops asio*) hatching three Wood Duck (*Aix sponsa*) eggs in a suburban nest box. Wood Duck(s) removed all five eggs of a completed screech-owl clutch, the earliest of which had already been incubated for at least 19 days, and laid three eggs in their place. The female screech-owl hatched the Wood Duck eggs, preened the ducklings, and attempted to feed them until they exited the nest box within 48 hrs of hatching. *Received 22 December 2005. Accepted 27 July 2006.*

Wood Ducks (*Aix sponsa*) are well known to lay parasitically with conspecifics (Hartman 1972, Semel and Sherman 1986) and other cavity-nesting ducks (Bouvier 1974, Eadie et al. 1998). Wood Ducks occasionally remove conspecific eggs; however, such records usually involve damaged eggs (Semel and Sherman 1986). Wood Ducks are reported to "evict" other bird species including screech-owls from nest boxes (Bellrose and Holm 1994). However, Semel and Sherman (2001) report that when returning female Wood Ducks found boxes in which they had previously nested occupied by heterospecifics, including Eastern Screech-owls (*Megascops asio*), they switched to another box ($n = 10$). Here I record Wood Duck(s) removing an entire clutch and laying in a nest of Eastern Screech-owls.

OBSERVATIONS

While studying the reproductive ecology of Eastern Screech-owls in suburban Winnipeg, Manitoba, I installed a miniature video camera in May 2004 inside a nest box in which a pair had successfully reared broods in two previous years. Five chicks fledged from this box in 2004. A female began laying on 3 April 2005 and by 10 April was incubating a clutch of five eggs. There was no sign of any unusual activity at the nest until 22 April, when observers noted there were only three screech-owl eggs and one much larger egg. On 23 April, there was a second large egg and the three remaining owl eggs (Fig. 1A). On 24 April no change was noted; however, on the morning of 25 April, two more owl eggs had been removed and a third larger egg was present (Fig. 1B). Video recordings were made on a nightly basis but, unfortunately, did not extend sufficiently into the morning to record the removal of eggs. I monitored the nest box from 0600 to 0730 hrs CST for the next 3 days and, on each morning, a pair of Wood Ducks landed close to the box. The female Wood Duck then flew to the roof of the box and stepped repeatedly and heavily on it before making a short circular flight and landing on the entrance hole. On each occasion I observed this behavior, the incubating owl jumped up to prevent the duck's entrance. On 27 April, a female Wood Duck was recorded gaining entrance to the nest box at 0638 hrs but was expelled by the owl which tried to bite the intruder on the back of the neck. On the morning of 2 May, the remaining owl egg was removed, although no new Wood Duck eggs were added. Unfortunately egg removal was not recorded due to a technical difficulty.

I concluded the larger eggs in the box were Wood Duck eggs (confirmed upon hatching; Helgeson Nelson 1993). There was no evidence of any damaged eggs in the box and no eggs had been buried in the nesting material. The edge of the Red River was only a few meters from the base of the nest tree and, because there were no eggs or shells below the box, the removed eggs may have been dropped over water or consumed (Semel and Sherman 1986).

Despite the absence of her own eggs, the female owl incubated the three Wood Duck eggs. The first egg hatched at 2240 hrs on 25 May, the other two hatched later that evening. Shortly after hatching, the owl preened the

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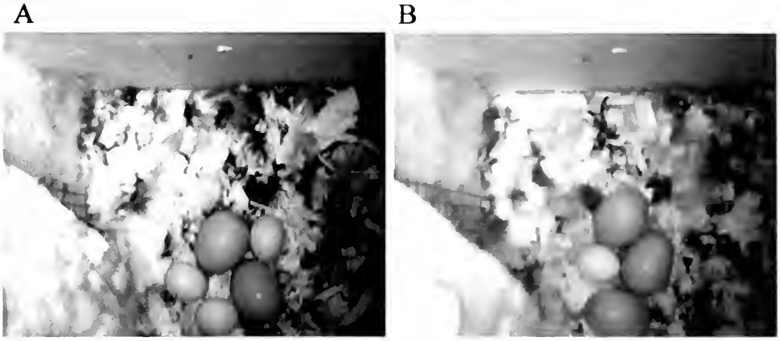

FIG. 1. (A) Three Eastern Screech-owl eggs and two Wood Duck eggs on 24 April 2005; (B) One Eastern Screech-owl egg and three Wood Duck eggs on 25 April 2005, Winnipeg, Manitoba. The wing and tail of the female screech-owl sitting at the box entrance are visible in the lower left corner in both images.

ducklings and ate pieces of eggshell. She also brooded and attempted to feed the chicks. When the ducklings attempted to exit the box, the female owl gave whinny calls, which are "elicited particularly by dispersing juveniles" (Gehlbach 1995:7). The first chick exited the box just before 2200 hrs on 26 May and the second shortly afterwards. The third chick departed the box at 0730 hrs on 27 May. The property owner took one duckling to a local nature reserve, but the other two were not located. Wood Duck chicks are highly precocial and brood merging has been recorded (Kirby 1990), but it is not known whether the chicks in question survived.

DISCUSSION

Raptorial birds occasionally incubate waterfowl eggs. Dawson and Bortolotti (1997) reported an American Kestrel (*Falco sparverius*) incubating a Bufflehead (*Bucephala albeola*) egg and four kestrel eggs (the Bufflehead and two kestrel chicks fledged). Fannin (1894) reported a mixed clutch of Canada Goose (*Branta canadensis*) and Osprey (*Pandion haliaetus*). The Black-headed Duck (*Heteronetta atricapilla*), an obligate brood parasite, at times parasitizes diurnal raptors (Weller 1968, Höhn 1975). Wood Duck eggs have occasionally been found in nests of Western Screech-owls (*Megascops kennicottii*) (J. M. Eadie, pers. comm.). In Winnipeg, Manitoba there are several records from volunteers of the Fort Whyte Nature Centre of joint use of nest boxes by Eastern Screech-owls and Wood Ducks (e.g., on 11 April 1997, 1 Eastern Screech-owl egg, 5 Wood Duck eggs, and 7 membranes were found in one box). This does not imply synchrony of use because some may have been from the previous year or sequential nesting, and it is possible that dumping or usurpation may have occurred. Eastern Screech-owls have been recorded incubating the eggs of other species (Breen and Parrish 1996). Manlove (1998) reported an Eastern Screech-owl apparently evicting a nesting Wood Duck, laying on top of the covered duck eggs, and subsequently hatching at least one owlet and one duckling.

The average incubation periods for both Eastern Screech-owl and Wood Duck are approximately 30 days (Gehlbach 1995, Hepp and Bellrose 1995). In this case, the female owl sat on the Wood Duck eggs for 31–34 days, within the normal range of incubation for Wood Ducks (25–37 days) (Hepp and Bellrose 1995). However, because the owl initiated egg laying much earlier than the Wood Duck(s), her eggs would have hatched approximately 3 weeks before any of the duck's had they not been removed. By accepting the Wood Duck eggs, the female owl's total incubation period was extended to 55 days. Eastern Screech-owls have been recorded incubating infertile eggs for as long as 78 days (Gehlbach 1995).

Incidental egg dumping has been recorded in many avian species (e.g., Sealy 1989). However, the removal of host eggs over a 10-day period suggests this was not a case of egg dumping. A failed attempt at nest usurpation, however, cannot be dismissed. Unusual interspecific interactions of this nature have been attributed to competition for nest sites (Eadie et al. 1988), but several studies suggest that nest parasitism in Wood Ducks is not related to a lack of cavities (Semel and Sherman 1986). Dawson and Bortolotti (1997) argued that certain desirable qualities of the nest site might be a factor. In this case, there was a vacant nest box in the same yard with no discernable structural differences in which Wood Ducks had previously reared several broods. Semel et al. (1988) demonstrated that conspicuous placement of nest boxes increased intraspecific nest parasitism rates in Wood Ducks and the box in question was highly visible. This serves as a reminder, perhaps, of the caution required when artificial nesting structures are used as management tools (Eadie et al. 1998).

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Observation of an Extra-pair Copulation by Sandhill Cranes

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ABSTRACT.—This paper describes an extra-pair copulation (EPC) event between two color-banded Sandhill Cranes (*Grus canadensis*). This is the first documented occurrence of an EPC during the fertile period of Sandhill Cranes. This event adds to the small list of documented EPCs in long-lived bird species with long-term pair bonds. Participating in an EPC may have allowed the female to potentially gain access to a mate with a breeding territory, something she did not have during the previous two breeding seasons. Benefits to the male may have included increasing his reproductive success without having to raise the offspring or evaluating the female as a potential new mate. *Received 24 October 2005. Accepted 12 July 2006.*

Extra-pair copulations (EPC: copulations outside an established pair bond) are an alternative mating strategy used by many monogamous bird species. There are striking differences between males and females in benefits acquired by participating in EPCs (summarized in Griffith et al. 2002). Males may benefit from EPCs by increasing the number of offspring through extra-pair fertilizations (EPF) without the need for investment of resources to raise them, while females may use EPCs to increase the reproductive fitness of her offspring by acquiring "good genes" or morphological traits, or to gain access to resources. Both males and females may use EPCs to guard against a current mate's low fertility or to evaluate the quality of a future mate.

Evidence of EPCs in wild birds has been strong in monogamous species with short-term pair bonds that often last for only one breeding attempt (Westneat and Sherman 1997, Petrie and Kempenaers 1998, Arnold and Owens 2002). Many of these species are short-lived and it may be advantageous to seek extra breeding opportunities. In long-lived species with long-term pair bonds and shared parental investment, records of EPCs are rarer. Mills (1994) suggested that birds with these life history characteristics should spend more time maintaining and strengthening their pair bond rather than actively searching for EPCs. In waterfowl, EPCs are common via forced copulation through use of intromittent organs (McKinney et al. 1983, Afton 1985, Davis 2002). In Oystercatchers (*Haematopus ostralegus*), EPCs were common before nest initiation, while members of established territorial pairs copulated together the month prior to laying eggs (Heg et al. 1993). Frequency of EPF was only 1.5% of 65 chicks tested; the father was a male from a nearby territory (Heg et al. 1993). Two other female oystercatchers used EPCs to find a new mate (Heg et al. 1993).

Sandhill Cranes (*Grus canadensis*) are long-lived, highly territorial, and form long-term pair bonds (Walkinshaw 1973). Incubation takes about 30 days and both members participate relatively equally (Walkinshaw 1973). Aside from when one mate is incubating, pairs are typically observed together during the breeding season and sometimes throughout the year (Tacha et al. 1992). Although cranes have a defined breeding season (i.e., only fertile during a specific time period each year; Archibald and Lewis 1996), copulation between pair members can occur prior to (Littlefield 1985) and following the normal breeding season (MAH, pers. obs.). Frequent copulation may serve to reinforce long-term pair bonds (Voss 1976). Although EPCs during the breeding season have not been documented for Sandhill Cranes, females have solicited males while their mates were incubating (Nesbitt and Wenner 1987; A. E. Lacy, pers. comm.). Further, a female acted paired with two different males, oscillating between them 20 times during a 12-month period; she

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was only observed nesting with one of the males (Nesbitt et al. 2001).

The observed EPC occurred in a breeding population of Sandhill Cranes near Briggsville, Wisconsin (43° 36′ N, 89° 36′ W), a matrix of agriculture and wetland systems with limited residential, industrial, or commercial development (Su 2003). The International Crane Foundation (ICF) has been color-banding (Hayes et al. 2003) and monitoring this population for over 14 years to study breeding biology (Hayes 2005) and habitat requirements (Su 2003). The area is densely populated with breeding pairs and nonbreeding flocks composed of sexually immature subadults, sexually mature adults that may be paired, but not yet defending a territory (Walkinshaw 1973), and former breeding adults that lost their territories following divorce or mate loss (Nesbitt and Wenner 1987, Nesbitt and Tacha 1997, Hayes 2005). Initial pair bonds are formed within nonbreeding flocks (Walkinshaw 1973, Nesbitt and Wenner 1987). Frequency of EPF in this population was between 4.4 and 11.1% for 45 chicks and between 5.6 and 22.2% of 18 family groups using microsatellite DNA markers (Hayes et al. 2006). Thus, EPCs are occurring, but at an unknown frequency.

OBSERVATIONS

The EPC occurred between two banded individuals with known breeding histories. The participating male (#363) has been on territory with an unbanded female since at least 1997 (when he was captured). Male #363 fledged only one chick (in 1999) with an unbanded mate. The participating female (#135) was captured with her mate (#136) and fledged chick in 1996. Although this pair produced chicks in 1997 and 1998, none fledged. Male #136 was last observed in November 1998. In late April 1999, female #135 was present in the study area, but was not defending her territory because a new unbanded pair was present. Female #135 was observed in a nonbreeding flock of four birds consisting of a banded un-paired male hatched in 1996 (#123), a banded un-paired male hatched in 1997 (#137), and an unbanded bird of unknown gender or age. This group was observed regularly throughout 1999 and spring 2000. On 7 June 2000, female #135 and male #123 conducted a unison call (an antiphonal duet between a male and female crane; Archibald 1976), suggesting a pair bond was forming. Neither male #137 nor the unbanded bird was present at the time. Three days later, the four-bird group was reformed. In August 2000, female #135 was observed unison calling multiple times with male #123 over a 5-day period. Male #123 and female #135 did not defend a territory while paired.

On 14 March 2001, male #363 and female #135 were observed as a pair on male #363's territory. Male #363's former unbanded mate was not observed. On this day, male #363 and female #135 first unison-called, male #363 mounted female #135 and the pair copulated for 2–3 sec, followed by ritual preening (Archibald and Lewis 1996), all signs of an established territorial pair. The extent of cloacal contact was difficult to ascertain (due to tall grass), but extensive copulation behavior suggests the pair was intent on reproduction, and this event represents an EPC. Although this was early in the breeding season for this population (ICF, unpubl. data), female cranes can store sperm up to 9 days and produce fertile eggs (Jones and Nicolich 2001). Chicks only 1–3 days of age have been observed in this population as early as the last week in April (ICF, unpubl. data).

On 15 March, male #363 was observed on territory with an unbanded female, presumed to be his former mate. This pair was observed incubating a nest in April but failed to produce chicks. Female #135 was not located again until 10 April, when she was paired with an unbanded male (without chicks) near male #363's territory. From 14 April to 31 May, female #135 was observed alone intermittently, suggesting that she and her unbanded mate could be nesting, but this could not be ascertained from subsequent observations because no chicks were observed. On 24 May, male #363 chased female #135 from his territory where she was foraging. Because no chicks were observed with either pair, the presence of EPF could not be verified. Female #135 has not been observed since July 2002. It is possible she moved outside of our study area or died. Male #363 was still with an unbanded mate and defending the same breeding territory, fledging a chick in 2006.

DISCUSSION

Potential reasons for the EPC may differ between the participating male and female. Female #135 had not held a territory for two consecutive breeding seasons prior to the event. Non-territorial cranes have not been observed breeding in this population (J. A. Barzen, pers. comm.). Mating with male #363 likely represented an attempt by female #135 to establish a pair bond to gain access to a territory (Kempenaers and Dhondt 1993, Griffith et al. 2002). It is less likely she was attempting to solely gain "good genes" from male #363 or guard against her current mate's low fertility (Kempenaers and Dhondt 1993), as she did not have a breeding territory or mate when the event occurred. Although she paired with male #123, the pair did not defend a territory. Any benefit to male #363 from the EPC is less clear. Male #363 could have been trying to increase his fitness through an EPF (Gibbs et al. 1990, Westneat 1990). At least one female Sandhill Crane has used EPF to increase her reproductive success without losing her mate or territory (Hayes et al. 2006). Male #363 may also have been evaluating female #135 as a new mate (Heg et al. 1993), but this clearly did not occur. Whether he decided not to choose her or his current mate drove female #135 away is unknown. He was observed, however, chasing female #135 from his territory within this same breeding season.

While an isolated event, this observation provides documentation of EPCs in Sandhill Cranes. The actual frequency of EPCs in Sandhill Cranes is unknown. EPC's could result from an unstable pair bond, leading to a mate switch (Nesbitt and Wenner 1987, Heg et al. 1993). Temporary divorces, resulting from asynchronous migration (Hayes 2005), may cause a pair member to take a new mate as insurance against a previous mate not returning. Temporary divorces could lead to EPCs prior to original pair members reuniting on the breeding grounds. It is possible the frequency of EPCs may be higher in this population of Sandhill Cranes, but have gone undetected because copulations are rarely observed as our behavioral sampling is not sufficiently intensive to readily detect these events.

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Novel Snowy Egret Foraging Behavior

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ABSTRACT.—We observed five Snowy Egrets (*Egretta thula*) on 23 October 2005 swimming and feeding in a small constructed wetland in Boca Raton, Florida. This event occurred 5–10 m from the shoreline in water >1 m in depth over a 2-hr period. We provide the first detailed account of *swimming feeding* behavior for Snowy Egrets. Elevated numbers of prey fishes at the surface of the pond may have facilitated this previously undocumented feeding behavior of Snowy Egrets. *Received 21 November 2005. Accepted 28 July 2006.*

Snowy Egrets (*Egretta thula*) have been reported to use an assortment of foraging behaviors previously defined by Kushlan (1976), Willard (1977), Kasner and Dixon (2003), and Kelly et al. (2003). Kelly et al. (2003) described 34 foraging behaviors, of which Snowy Egrets used 29, detailing their plasticity when feeding. *Swimming feeding* remains one of the five published wading bird foraging behaviors that Snowy Egrets have not been documented using, although Great Egrets (*Ardea alba*), Great Blue Herons (*A. herodias*), Tricolored Herons (*E. tricolor*), and Green Herons (*Butorides virescens*) have used this behavior (Kushlan 1976, Willard 1977, Kasner and Dixon 2003, Kelly et al. 2003).

We observed five Snowy Egrets *swimming feeding* on 23 October 2005 from 1700 to 1900 hrs EST in a small (~5,000 m^2) constructed wetland in a housing subdivision in Boca Raton, Florida (26° 21′ N, 80° 04′ W). Snowy Egrets and Tricolored Herons used *swimming feeding*, where they flew 5–10 m from shore, landed in the water and proceeded

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to capture fish on or within 5 cm of the surface while swimming. Both species extended their head under the water at least 15 cm on several occasions. Snowy Egrets and Tricolored Herons appeared to be successful in capturing fish with each attempt, but we did not quantify capture rates. Fish captured by both Snowy Egrets and Tricolored Herons using this technique were approximately 3 cm long on average based on heron bill lengths (Frederick 1997, Parsons and Master 2000). Both species would take off and fly to the shoreline after capturing prey, where they either rested or began feeding along the water's edge. The Snowy Egrets were foraging in a mixed flock (~20 birds) of Great Egrets, Tricolored Herons, and Wood Storks (*Mycteria americana*). All species were observed feeding along the shoreline but Great Egrets, Snowy Egrets, and Tricolored Herons also foraged in the open water, using either *plunging* (all three species) or *swimming feeding* (Snowy Egret, Tricolored Heron) behaviors.

Numerous small (<5 cm) fish were observed surfacing during the period that Snowy Egrets and Tricolored Herons used the *swimming feeding* behavior. The surfacing behavior of the fish may have been due to emerging aquatic insects, unobserved piscine predators, or perhaps low dissolved oxygen levels, requiring surface respiration by fish (e.g., mosquito fish, *Gambusia* spp.). This pond was normally aerated to prevent growth of algae but our observation occurred during an electrical power outage, which may have result in lowered dissolved oxygen levels. Searcher species are well suited to locating and exploiting ephemeral food patches (Gawlik 2002), possibly caused by the power outage. Kersten et al. (1991) showed that Little Egret (*E. garzetta*), a similar species in appearance and behavior (Parsons and Master 2000), quickly exploited increased prey availability resulting from anoxic water conditions that occurred for only a short period of time each day. The frequency of this feeding behavior in Snowy Egrets is apparently quite low, as it was previously undocumented and likely does not have an important role in prey acquisition except under such exceptional circumstances.

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Wild Great Hornbills (*Buceros bicornis*) Do Not Use Mud to Seal Nest Cavities

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ABSTRACT.—The literature pertaining to nesting of the Great Hornbill (*Buceros bicornis*) is ambiguous regarding whether the birds use mud as plaster material to seal their nest cavity entrances. We studied the breeding biology of the species in southern India and detected no evidence of mud delivery or usage in 183 hrs of nest observations. Chemical analysis of plaster material showed that it was composed exclusively of fecal material and not mud. *Received 15 May 2006. Accepted 9 August 2006.*

The Great Hornbill (*Buceros bicornis*) is a large, principally frugivorous, and endangered species of south- and southeast Asian rainforests. Its nesting habits are largely typical of the family. The female becomes sealed in a tree cavity and remains in confinement during incubation and for a period after hatching of the chick (Kannan 1994, Kannan and James 1997). There is considerable ambiguity in the literature concerning whether the species uses mud in sealing its nest cavities. Some authors indicated that mud was used, some were uncertain if mud was used, and some categorically stated that mud was not used. No quantitative evidence exists and statements made by previous authors have been based mostly on anecdotal observations. Hume (1890: 69), quoting others who observed the nesting behavior of the species in Burma (Myanmar), indicated the nest entrance was "covered with a thick layer of mud." Hume (1890: 70) also included nebulous statements attributed to others about "the male plastering the female in with his ordure" and the plaster being "composed of dung and earth." Bingham (1897: 309) wrote that all five nests he examined in Burma had their entrance covered with "a plastering of earth leaf-mould and the birds' own droppings." Poonswad et al. (1987: 260) presented a rough composition of sealing material from adjacent Thailand, which showed earthen material only in miniscule amounts, the rest being "wood dust, piece of wood, (and) food debris", about one-third each. Baker (1927: 285, 1934: 429) stated that the male "sometimes, but not always" brings wet mud, remains of fruit, and his own droppings. Ali and Ripley (1970: 145), describing the race *B. b. homrai* of southern India, indicated the nest entrance was an amalgam of the female's dung and remains of figs, bits of leaves and sticks, "possibly supplemented with wet mud brought by the male." Kemp (1995: 181), describing the species' habits, wrote that it hops when on the ground to feed on fallen fruit, to search for animals along stream banks, "or to collect soil for sealing." He also wrote the nest entrance is sealed with droppings, chewed pieces of wood and bark, food and nest debris, but "little if any soil." The species has been observed to descend to the ground occasionally to collect fallen fruit (Ali and Ripley 1970), but Kemp's (1995) description of it collecting soil from the ground is the only mention in the literature. Datta (2001) was the only report that unequivocally stated no mud usage in a 4-yr study (416 hrs of observations) involving eight nests in northeast India. All nests in her study were sealed with fecal material of the female, which was comprised mainly of fig seeds (Aparajita Datta, pers. comm.).

The ambiguity also extends into the literature on captive breeding accounts of the Great Hornbill. Stott (1951: 114) wrote the material used by the species during an unsuccessful breeding attempt in the San Diego Zoo was gray and apparently non-granular in texture, "and may well have included among its components the fine sand that had been placed in

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TABLE 1. Composition (%) of Great Hornbill nest plaster (obtained from the Western Ghats of southern India), feces, and top soil.

	Chemical elements							
	P	K	Ca	Mg	S	N	Total ash	Total organic
Hornbill plaster[a]	0.2	2.1	1.5	0.3	0.2	2.0	15	85
Chicken feces[b]	1.3	1.2	2.9	0.6	0.8	5.0	8[c]	92
Cattle feces[b]	0.7	1.7	2.9	0.6	0.2	2.0	19[d]	81
Tropical soil[e]						0.2	96	4

[a] Present study.
[b] Spector 1956 (Table 159).
[c] Gerry 1968.
[d] Ensminger et al. 1990.
[e] Sanchez 1976.

the bottom of the nesting barrel." Poulsen (1970) and Choy (1980) reported a mixture of mud, the birds' feces, and mashed fruits as plaster material used in zoos in Denmark and Singapore, respectively. (The former breeding attempt was abandoned after partial nest sealing, and the latter was successful). Reports from three other captive breeding attempts (all successful), one in the United Kingdom (Golding and Williams 1986), and two in the United States (Bohmke 1987, Thormahlen and Healy 1990), unequivocally indicated no mud was used in the sealing process. Golding and Williams (1986) and Bohmke (1987) did not say whether mud was made available to the birds, but Thormahlen and Healy (1990) stated that mud was not provided.

Darwin (1871: 778) reported "The female Horn-bill (*Buceros*) . . . plasters up with her own excrement the orifice of the hole in which she sits on her eggs." This is an apparent early confirmation that only excrement constituted the plaster. He quoted the earlier observation of Horne (1869). However, inspection of the paper by Horne (1869) shows he was referring to the Indian Grey Hornbill then named *Meniceros birostris* now *Ocyceros birostris* (Grimmett et al. 1999), which Horne incorrectly gave the trivial name *bicornis*. Darwin incorrectly thought Horne was describing *Buceros bicornis*.

OBSERVATIONS

We observed a nest of the Great Hornbill in the Anaimalai Hills of the Western Ghats of southern India in 1992 and 1993. We found no evidence of mud delivery or usage in 183 hrs of observation. The female was observed to only use her feces as plaster material. After exit of the female, the chick was observed to use exclusively its feces for resealing the entrance. The male did not participate in nest sealing (Kannan 1994, Kannan and James 1997).

We verified these observations by collecting broken chunks of plaster that had fallen to the ground on the fecal midden at the base of the nest tree and had the chunks analyzed for chemical element composition, total ash, and organic components at the Agricultural Services Diagnostic Laboratory, University of Arkansas, United States. The values obtained were compared with published information on the properties of tropical soil, chicken feces, and cattle feces (Table 1).

The data from the plaster sample matched the chemical composition of chicken and cattle fecal material (Spector 1956, Gerry 1968, Ensminger et al. 1990), and was different (Table 1) from the low nitrogen, high total ash, and low total organic content of tropical soil (Sanchez 1976). Thus, the plaster used to seal the nest cavity opening was wholly fecal material without an admixture of soil. Chicken fecal matter was included (Table 1) to represent a bird and cattle manure was added to characterize an animal with a vegetarian diet to compare with the fruity and mainly vegetarian diet of the hornbill (Kannan 1994).

DISCUSSION

There are three possible reasons for the ambiguity in the literature about hornbill sealing material. First, early authors such as Hume (1890) could have mistaken the sealing material to be mud because of its earthen appearance. Ali and Ripley (1970) noted the plaster dries to the consistency and appearance of sunbaked clay. Second, some authors may have merely assumed mud to be involved because use of mud is widespread in other species in the family (Kemp 1979, 1995). This error may have been perpetuated in subsequent writings. The commonly used phrase for plastering, "mudding up", (used by Golding and Williams [1986] who reported no mud!), may have further contributed to this assumption. Finally, it is possible this species uses mud opportunistically when the need arises. Captive birds use mud only when cementing material such as rotting wood, wood shavings, and squashed fruit are not available (Thormahlen and Healy 1990; S. Y. Healy, pers. comm.). Captive birds may need cementing material in addition to their feces because they are usually offered a diet of mixed soft fruits (Christine Sheppard, pers. comm.). This renders their excreta poor in tiny seeds such as fig (*Ficus*) found abundantly in feces of wild birds. One report from captivity indicated a chronic problem of the plaster failing to adhere properly to the cavity opening (Thormahlen and Healy 1990). Thus, an opportunistic inclusion of mud in the plastering material seems plausible in captivity. Mud usage in the wild is highly unlikely because the myriads of tiny fig seeds in the feces apparently hold the plaster together "much like gravel in a concrete mix" (Kannan and James 1997: 455). This makes mud or any cementing mixture other than its own feces unnecessary. The issue of whether mud is used in captivity and if mud should be furnished to captive birds may have conservation implications because captive breeding of endangered hornbills is one of the proposed ways to manage these species (Kemp 1995).

Kemp's (1995) assertion that wild Great Hornbills descend to the ground to collect mud for sealing is probably based on a logical assumption (i.e., if the birds use mud, they have to get it from the ground) rather than direct observation. We did not observe Great Hornbills descend to the ground in two years of intense observations in the wild. With the exception of Datta (2001), all studies on wild birds indicated use of mud as sealing material. Our field observations, albeit from just one nest, are supported by those of Datta (2001) from multiple nests. Our chemical analysis data and field observations, and the fact that the species has not been reliably observed in the wild to collect mud from the ground, indicate that wild Great Hornbills do not use mud for plastering their nest cavity entrances, but instead exclusively use fecal material.

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First Description of the Nest, Eggs, and Breeding Behavior of the Mérida Tapaculo (*Scytalopus meridanus*)

Karie L. Decker,[1,2] Alina M. Niklison,[1] and Thomas E. Martin[1]

ABSTRACT.—We provide the first description of the nest, eggs, and breeding behavior of the Mérida Tapaculo (*Scytalopus meridanus*). Data are from one pair in the moist cloud forest of Yacambu National Park, Venezuela during April–May 2004. Two nests, constructed by the same pair, were globular in structure and consisted of mossy material placed in a rock crevice of a muddy rock wall. The eggs were cream colored with an average mass of 4.19 g. Clutch sizes were one in the first nest and two in the second. The species showed bi-parental care in nest building and incubation. Nest attentiveness (percent time spent on the nest incubating) averaged 83.4 ± 14% (SD). Average on and off bouts were 33.24 and 6.34 min, respectively. *Received 22 December 2005. Accepted 11 August 2006.*

Breeding biology and life history traits of tropical birds remain poorly known. Nests have not been found nor described for many species limiting our knowledge and understanding of tropical life histories. Of approximately 40 currently recognized species of *Scytalopus*, nests of ~12 species have been described (Sclater and Salvin 1879; Skutch 1972; Stiles 1979; Hilty and Brown 1986; Sick 1993; Krabbe and Schulenberg 1997, 2003; Christian 2001; Young and Zuchowski 2003; Greeney and Gelis 2005; Greeney and Rombough 2005). *Scytalopus* is found throughout the Andes from Central America to Tierra del Fuego Island (Fjeldså and Krabbe 1990, Krabbe and Schulenberg 2003). We present data on life history traits (nest description, clutch size, egg mass, nest building, egg laying, and incubation investment) of *Scytalopus meridanus* in Yacambu National Park, a wet cloud forest of north central Venezuela (09° 42′ N, 69° 42′ W; 1,900 m elevation).

Scytalopus are elusive birds, often only detectable by sound (Hilty et al. 2003, Krabbe and Schulenberg 2003). *Scytalopus meridanus*, a small 16.5-g bird, similar to a wren, is

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known to scuttle on the ground among thick brush and grasses (Hilty et al. 2003). We observed individuals within 30 m of a creek, foraging low to the ground with short, rapid movements. Their call is a series of 25–30 quick sharp monotone 'wick' notes, similar to that of the Northern Flicker (*Colaptes auratus*), repeated for 10–15 sec.

OBSERVATIONS

The first nest, found on 16 April 2004, was 0.8 m above a creek bed in an obscured crevice about 6.25 cm deep into a muddy, rock face. The globular nest was at the end of this crevice and was composed of moss, rootlets, and decomposing leaves. The inside diameter and height were 6.8 and 6.2 cm, respectively, while the outside diameter and height were 10.5 and 8.5 cm, respectively. Incubation had commenced prior to finding the nest and the adults were incubating a single, cream-colored egg of unknown age with a mass of 4.07 g. We monitored the nest for 5 days during the incubation period until it was depredated on 21 April, and videotaped it once for 5.75 hrs (17 Apr, 0705–1345 hrs EST) following Martin (2002). In the video, *S. meridanus* exhibited simultaneous incubation exchange, revealing that both male and female incubate. Nest attentiveness (percent time spent on the nest incubating) averaged 82.2%, while incubation bouts averaged 33.13 min (n = 11); the mean off bout length was 7.26 min (n = 11).

The second nest, a re-nest of the same pair, was located on 4 May 2004 approximately 15 m from the first nest. The nest was 1.2 m above the bottom of the creek bed, in a similarly concealed crevice 7 cm deep, and constructed from similar material. The nest contained one egg when found and, after checking the nest daily for eight days, another egg was laid. The day the second egg was laid (12 May), the eggs of the second nest weighed 4.38 and 4.12 g. We videotaped the nest three times: once during the laying period and twice during incubation, totaling nearly 19 hrs (7 May, 0741–1345; 15 May, 0732–1352; and 23 May, 0711–1346 hrs). The first video revealed that during the laying period, both adults continued to build the nest after one egg had been laid. Both parents repeatedly brought small mossy material to the nest. In addition, both adults appeared to intermittently incubate the single egg, but had an average attentiveness of only 45.2%. This incubation activity occurred only during the cool early hours between 0741 and 0920 hrs. From 0921–1345 hrs, the parents visited the nest only briefly, bringing nesting material, but did not incubate. The two incubation videos revealed that nest attentiveness on the third day of incubation (15 May) and the eleventh day (23 May) was comparable to that of the first nest of unknown incubation age (percent time on = 82.6 and 84.8%, respectively). Mean on and off bout lengths during first and second incubation videos (37.20 min on, 7.34 min off; and 29.38 min on, 4.43 min off, respectively) also were similar to the first nest. We monitored the nest daily for 8 days before the second egg was laid (4–12 May), and for 13 days after (12–25 May), until depredated, at which point the eggs had not yet hatched. The incubation periods documented for other *Scytalopus* are 15–23 days (De Santo et al. 2002, Krabbe and Schulenberg 2003); the period that we monitored this nest is well within this range.

DISCUSSION

Life history traits have been described for only a few other species of *Scytalopus*. Egg color and shape were similar to most other *Scytalopus* described to date, as was clutch size (Stiles 1979, Whitney 1994, De Santo et al. 2002, Krabbe and Schulenberg 2003). Nest composition, placement, and shape were consistent with other tapaculos (Stiles 1979, Whitney 1994, De Santo et al. 2002, Krabbe and Schulenberg 2003, Young and Zuchowski 2003, Greeney and Gelis 2005, Greeney and Rombough 2005). Many tropical birds have been reported to lay eggs on alternating days, some even with three days separating egg laying (Skutch 1976). Unlike any passerine of which we are aware, *S. meridanus* laid a second egg nearly one week after the first. We do not know if this pattern is typical, but may result from the large investment in eggs. Few records report detailed information on parental investment. We observed fairly high nest attentiveness not atypical of shared incubators (Martin 2002; TEM, unpubl. data). *Scytalopus meridanus* is sexually monomorphic and we could not ascertain if parents contributed evenly in nest attentiveness. However, length

TABLE 1. Reproductive attributes (means) of *Scytalopus meridanus* in Venezuela, 2004 (this study) and four other congenors in Central and South America (Krabbe and Schulenberg 2003).

Species	Clutch size	Egg volume (cm^c)	Egg mass (g)	Adult mass (g)	Egg mass/body mass (%)
S. meridanus[a]	1–2	4.064	4.190	16.5	25.39
S. speluncae	2	2.897	2.987[b]	13.75[c]	21.72
S. indigoticus	2	3.006	3.099[b]	14.80[c]	20.94
S. magellanicus	2–3	3.179	3.278[b]	11.00[c]	29.80
S. griseicollis	2	2.531	2.609[b]	17.97[c]	14.52

[a] Sample sizes for *S. meridanus* are: clutch size (2), egg mass/volume (3), and adult mass (1).

[b] Egg mass calculated from measurements reported in Krabbe and Schulenberg (2003) (sample sizes not given) using the equation in Van Noordwijk et al. (1981).

[c] Information from descriptions in Krabbe and Schulenberg (2003) (sample sizes not given).

of alternating bouts of different individuals appeared similar.

Scytalopus meridanus laid remarkably large eggs relative to the size of the 16.5-g adult (Martin et al. 2006), about 25% of its body weight. We could not locate egg mass records for other species of *Scytalopus*, but egg length and width measurements as well as adult mass were available for four species (Krabbe and Schulenberg 2003). We developed a relative coefficient (1.031) between mass and volume using egg length, width, and mass measurements from nine passerine species in Argentina (TEM, unpubl. data) to estimate egg mass. We inserted this coefficient to get the equation: mass = $(0.5 \times \text{length} \times \text{width}^2) \times 1.031$ (adapted from Van Noordwijk et al. 1981). All five *Scytalopus* species appear to have relatively high reproductive investment in eggs, given their body mass (Table 1). The allometric relationship across other species in Venezuela (Martin et al. 2006) predicts an average egg mass of approximately 2.6 g based on the 16.5-g body mass of adult *Scytalopus meridanus*. This predicted egg mass is much less than that observed and indicates that *Scytalopus* lays a large egg, even compared with other tropical species.

Scytalopus joins the ranks of other species in endemic tropical families by having small clutch size and shared incubation that yields relatively high nest attentiveness. What may be unusual is the interval between laying eggs and the size of the egg.

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An Interspecific Foraging Association Between Nearctic-Neotropical Migrant Passerines in Bolivia

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ABSTRACT.—I present the first published record of a foraging association between Nearctic-neotropical migrant bird species during the austral summer in South America. I observed Barn Swallows (*Hirundo rustica*) and Cliff Swallows (*Petrochelidon pyrrhonota*) in February 2005 repeatedly foraging on aerial insects flushed by flocks of Bobolinks (*Dolichonyx oryzivorous*) settling onto soybean plants (*Glycine max*). Additional observations would be needed to distinguish this behavior between an opportunistic association and a commensal relationship. *Received 25 November 2005. Accepted 28 July 2006.*

Foraging associations assumed to be commensal between passerine species have been described within mixed species flocks (e.g., Hino 1998) and between non-flocking species (e.g., Willis 1972, Maxson and Maxson 1981, Robbins 1981). Here, I report the first documentation of a foraging association between two flocking Nearctic-neotropical migrant species during the austral summer.

On 11 February 2005 from 0900 to 1000 hrs EST in San Juan, depto. Santa Cruz, Bolivia, ~100 km northwest of the city of Santa Cruz, I observed a flock of ~1,000 Bobolinks (*Dolichonyx oryzivorous*) foraging in soybean (*Glycine max*) fields. This large aggregation consisted of a series of smaller (30–400 individuals) flocks that moved across the field by landing in the soybeans for 15–60 sec, lifting to 1–3 m above the soybeans, flying 25–50 m, landing again, and repeating this pattern. After each landing, ~10–30 Barn Swallows (*Hirundo rustica*) and 0–5 Cliff Swallows (*Petrochelidon pyrrhonota*) captured aerial insects above the Bobolink flock, foraging 1–5 m above the soybean canopy for 5–10 sec. During two subsequent walking transects (400 m), perpendicular to and intersecting the flight path of the Bobolink flocks, I flushed Pyralid moths (*Omiodes indicata* Fabricius) with every step. The other insect species that flushed above the canopy, the adult stage of the velvetbean caterpillar (*Anticarsia gemmatalis* Hübner), was not abundant. No other insect species were observed flying

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above the soybean canopy. The insect fauna on soybean leaves appeared to be species-poor and dominated by Pyralid moths, with species of Coleoptera and Homoptera occasionally noted.

The "following" behavior I observed is frequently used by swallows, which are known to follow mammals, birds, humans, and farm equipment that flush prey. In some cases, concentrations of animals serve as cues to swallows that indicate local concentrations of food resources (Brown and Brown 1995, 1999). Once a few individual swallows locate a food source, they may serve to attract more swallows, known as "local enhancement" (Brown 1988). My observation of swallows feeding on lepidopterans is unusual, as lepidopterans have been previously reported as comprising only a small fraction of the diet of Cliff and Barn swallows (Beal 1918). However, diet for these opportunistic feeders varies depending on availability of prey items (Brown and Brown 1995, 1999).

The association between the three species, if observed on a regular basis, could be an example of commensal insectivory, whereby the swallows increase their foraging efficiency, while Bobolink foraging efficiency is unaltered. Bobolinks are not known to forage on aerial insects and were not observed feeding above the soybean canopy. They were eating caterpillars on the soybean leaves (RBR, pers. obs.), indicating they were not competing with swallows for food resources. I did not observe interspecific aggression or other direct interactions between the Bobolinks and swallows, suggesting the swallows were not interfering with or otherwise altering Bobolink activity.

There are two ways that swallows might be increasing their foraging efficiency by following Bobolinks. However, I did not measure swallow foraging efficiency with, versus without, Bobolinks as "beaters" (Rand 1954). Bobolink flock activity appeared to invariably increase the number of prey flying per unit area (prey density), and swallows may have had a greater chance of locating prey, resulting in more capture attempts per foraging bout or per unit time (increased feeding rate, Brown 1988). Alternatively, when insects are forced to fly upon being flushed, the proportion of successful capture attempts per time spent foraging may be higher (increased success rate, Kushlan 1978).

This association was not sustained over time. On seven subsequent dates over 2 weeks, I observed monospecific flocks of Bobolinks using the same soybean field in the absence of swallows. On one of these dates, Bobolink flocks were also observed in two soybean fields ~3 km away, but swallows were not seen over or adjacent to the fields. I also observed swallows foraging over soybean fields in the absence of Bobolinks.

The association reported may occur sporadically in South American soybean fields when Bobolink and swallow distributions overlap spatially and temporally. Conditions under which this phenomenon may occur in soybean fields must include (1) caterpillars consumed by Bobolinks are available (e.g., after emergence and prior to application of insecticides), (2) flying insects preferred by swallows are available, and (3) Bobolink flocks are sufficiently large to flush prey in quantities that enable swallows to increase their foraging efficiency. Swallows may opportunistically use a "following" strategy to increase their foraging efficiency in different habitats with different beater species in South America.

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Interspecific Egg-dumping by a Violet-green Swallow in an Active Western Bluebird Nest

Danika Kleiber,[1,2,6] Jenne Turner,[1,3] Amber E. Budden,[1,4] and Janis L. Dickinson[1,5]

ABSTRACT.—We observed a Violet-green Swallow (*Tachycineta thalassina*) laying an egg in an active Western Bluebird (*Sialia mexicana*) nest. The Western Bluebird male and not the female, was aggressive to the Violet-green Swallow but the swallow remained to lay the egg. This is the first documented incidence of which we are aware involving altricial interspecific egg-laying during the nestling phase. We suggest the timing of this event was more consistent with incidental egg deposition, or egg-dumping, than brood parasitism or nest usurpation. *Received 13 December 2005. Accepted 24 July 2006.*

Observations of birds laying eggs in nests of other species are of interest because this behavior, when timed appropriately and directed at nests where parents fail to recognize foreign eggs and offspring, may be the starting point for evolution of interspecific brood parasitism. Other explanations for this behavior are nest usurpation and egg-dumping, which is the deposition of an egg into another species' nest without any specific adaptive function. We collected video footage of a Violet-green Swallow (*Tachycineta thalassina*) laying an egg in an active Western Bluebird (*Sialia mexicana*) nest containing nine-day-old nestlings at Hastings Natural History Reservation, Carmel Valley, California (36° 22′ N, 121° 34′ W). Nest boxes have been monitored at Hastings and nearby ranches as part of a long-term study of Western Bluebirds since 1983 (Dickinson et al. 1996). Western Bluebirds are the primary box-nesting species at this study site, but other secondary cavity nesters use nest boxes at lower frequencies, including Ash-throated Flycatchers (*Myiarchus cinerascens*), Oak Titmice (*Baeolophus inornatus*), House Wrens (*Troglodytes aedon*), Bewick's Wren (*Thryomanes bewickii*) and Violet-green Swallows (Table 1).

We conducted a study of parental feeding behaviors during spring 2005 using video to identify patterns of resource allocation within

TABLE 1. Frequency of nest box use by secondary cavity-nesting species at Hastings Natural History Reservation, Carmel Valley, California, from 1983 to 2004.

Species	Nests (*n*)	Total use (%)
Western Bluebird	1,860	69
Ash-throated Flycatcher	298	11
Oak Titmouse	204	8
House Wren	175	7
Violet-green Swallow	122	5
Bewick's Wren	2	<1
Total nesting attempts (at least one egg)	2,661	100

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the nest. The day before filming we replaced the natal nest box and nest material with a box of the same dimensions containing a Western Bluebird nest, but with a Plexiglas side to accommodate the camera. A video camera and small LED light were positioned within a sleeve connected to the nest box on the morning of filming, which began at approximately 0530 hrs PST. Tapes were set on short play and recorded for a period of 120 min. During the first recording an experimenter collected simultaneous observational data on parental activity from a blind approximately 30 m away. Following tape completion, a second tape was inserted to record an additional 120 min of nestling provisioning observations. No additional observational data on parental activity were collected from outside the nest.

OBSERVATIONS

We collected video data on 27 May 2005 from a Western Bluebird nest containing five nine-day-old nestlings and a single unhatched Western Bluebird egg. In this instance, the time stamp on the video unit failed, and observations were timed using the video counter and calibrated using the corresponding observational data. The video nest watch began at 0520:00 hrs. At 0711:53 hrs, a female Violet-green Swallow entered the nest box and sat in the far left corner at the top of the nest cup. At 0712:46, the Western Bluebird male entered the box and proceeded to peck at the Violet-green Swallow's head six times before leaving the nest box at 0713:03. The Violet-green Swallow responded to the pecking attack by tucking her head down and remaining still. After 5 sec, the female Western Bluebird fed a nestling from the box entrance. She appeared to ignore the Violet-green Swallow and entered the box only to turn around, leaving 11 sec after arrival. The adult male and female Western Bluebirds fed the nestlings twice more while the swallow was in the nest box, but did so without entering the nest. At 0721:41, the first video tape ended and the second was inserted. We estimated the time from the ending of the first tape and beginning of the second to be approximately 30 sec, and added that time to our calculations. The Western Bluebird adults did not enter the box again while the Violet-green Swallow female was present. At approximately 0733 hrs, the Violet-green Swallow left the nest box, leaving a white egg on the outer rim of the nest cup where she had been sitting. During the afternoon the video nest box and nest were replaced with the natal nest box and nest; the Violet-green Swallow egg was also transferred. When we returned to the nest the following day the Violet-green Swallow egg was lying broken in the bottom of the nest. There was no second Violet-green Swallow egg.

DISCUSSION

Three hypotheses are possible explanations for our observations: nest usurpation, brood parasitism, and interspecific egg-dumping. Nest usurpation is a possible explanation given that Western Bluebirds and Violet-green Swallows are both secondary cavity nesters whose breeding times overlap (Brown et al. 1992, Guinan et al. 2000). However, in this instance, timing of egg-laying and the observed behavior of the Violet-green swallow was not consistent with nest usurpation. Violet-green Swallows in our population use nest boxes at a low frequency (Table 1), but are common and presumably use natural cavities as nesting sites. Previously described nest usurpation interactions between Violet-green Swallows and Western Bluebirds do not match the behavior we observed. In Arizona, Brawn (1990) observed large groups of Violet-green Swallows taking over a nest box defended by a Western Bluebird, but a single Violet-green Swallow, such as we observed, was not successful in displacing Western Bluebirds. Successful use of a Western Bluebird box by a single pair of Violet-green Swallows has been observed, but was preceded by interspecific provisioning of the bluebird's young (Eltzroth and Robinson 1984).

Brood parasitism can also be ruled out due to improper timing of laying. We found no record of either intra- or interspecific brood parasitism by Violet-green Swallows in the literature (Brown et al. 1992). The placement of the egg outside the nest cup would be inconsistent with brood parasitism behavior.

It is more likely the Violet-green Swallow laid the egg because she was physiologically committed to do so but was unable to lay in her original nest, a behavior known as "egg-dumping" (Wiens 1971). There are many documented cases of interspecific egg-dumping in avian species not known for brood parasitic behavior (Bailey 1886, Holcomb 1967, Wiens 1971, Gustafson 1975, Cannell and Harrington 1984, Littlefield 1984, Carter 1987, Sealy 1989). Females may lay in another cavity because they are unable to approach their own cavity at the time of laying, due to the presence of a predator, nest usurpation, or other disturbance. Based on monitoring of nest boxes at Hastings Reservation, 11.2% of 98 Violet-green Swallow nests with at least one egg failed before hatching from 1983 through 2005. This small incidence of nest failure during laying and incubation is only partially attributable to predation, but indicates that infrequent nest predation or disturbance during laying could account for the behavior we observed. Although there are no data on conspecific nest usurpation in Violet-green Swallows, nest usurpation has been well documented in Tree Swallows (*Tachycineta bicolor*) (Leffelaar 1985).

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Western Bluebird Captures a Western Fence Lizard

Caitlin A. Stern[1,2]

ABSTRACT.—I observed a male Western Bluebird (*Sialia mexicana*) capture a western fence lizard (*Sceloporus occidentalis*), the first reported incidence of vertebrate-directed raptorial behavior in the Western Bluebird. There are no previously published reports of Western Bluebirds capturing vertebrate prey, although there is one previous report of a Western Bluebird carrying an unidentified lizard in the manner of a prey item, and a few reports of predation on vertebrates by the congeneric Eastern Bluebird (*Sialia sialis*). *Received 9 January 2006. Accepted 28 June 2006.*

Western Bluebirds (*Sialia mexicana*) are primarily insectivorous during the breeding season, and rely upon berry crops during winter (Guinan et al. 2000). Individual Eastern Bluebirds (*Sialia sialis*), a congeneric species,

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which is also primarily dependent upon insects and small fruits (Gowaty and Plissner 1998), have occasionally been observed capturing vertebrate prey, such as snakes (Flanigan 1971) and shrews (Pinkowski 1974). Beal (1915) reported the bones of lizards and tree frogs in the stomachs of Eastern Bluebirds, as did Bent (1949). Braman and Pogue (2005) found a dead, 8.3-cm-long flat-headed snake (*Tantilla gracilis*) in an Eastern Bluebird nest box, suggesting a past predation event. Of 217 Western Bluebird stomachs examined by Beal (1915), not one contained evidence of vertebrate prey. Herlugson's (1982) analysis of Western Bluebird stomach contents similarly yielded no evidence of vertebrate prey items, and adults were not observed delivering vertebrate prey to nestlings. Gaylord (1995) observed a male Western Bluebird carrying an unidentified lizard in his bill; however, she did not observe the capture or consumption of the lizard. There have been no previous reported observations of Western Bluebirds capturing vertebrate prey.

OBSERVATIONS

Western Bluebirds have been color-banded and their breeding biology monitored at Hastings Natural History Reservation, Carmel Valley, California, since 1983 (Dickinson et al. 1996). While censusing a winter group on 11 October 2005, I observed a first-winter male Western Bluebird catch a ~5-cm-long western fence lizard (*Sceloporus occidentalis*; Stebbins 1966) in his bill at 0928 hrs PST. The bluebird was perched on top of a wooden fence post, and the lizard was clinging to the side of the post ~7 cm below the bluebird. The bluebird left his perch, hovering briefly beside the post as he seized the lizard around its middle with his bill. This maneuver was executed quickly, and the lizard did not attempt to flee, although it arched its body after it was already held in the bluebird's bill. Returning to his perch on the same fence post, the bluebird twice beat the lizard's head against the post. This appeared to be an attempt to stun or kill the lizard. At 0930 hrs, the bluebird flew with the now immobile lizard still in his bill onto the property of a private ranch. I was not able to follow and ascertain whether the bluebird consumed the lizard because this ranch is closed to researchers.

DISCUSSION

Western Bluebirds commonly beat invertebrate prey against a perch before consumption, and both Flanigan (1971) and Pinkowski (1974) reported Eastern Bluebirds beating vertebrate prey items against perches before consuming them. The observed bluebird male was clearly treating the lizard as a prey item.

That vertebrate-directed raptorial behavior by Western Bluebirds has not been reported previously, despite intensive observation of Western Bluebird behavior, suggests that, similar to Eastern Bluebirds, Western Bluebirds rarely capture vertebrate prey. To my knowledge, capture of vertebrate prey by the third member of the genus *Sialia* (i.e., Mountain Bluebird, *Sialia currucoides*) has not been reported.

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Differences in Song Rate in Two Populations of Yellow Warblers

C. Morgan Wilson[1,2,4] and Rebecca L. Holberton[1,3]

ABSTRACT.—The Yellow Warbler (*Dendroica petechia*) has a mating system characterized by monogamy and biparental care, and has the broadest breeding distribution of any *Dendroica* species. When faced with a short breeding season and unpredictable conditions at high latitude, they display physiological responses to help optimize the tradeoff between individual risk and reproductive success. Because these circumstances may also affect behavior, we measured the song rates (songs/hr) of subArctic- and temperate-breeding males during the nestling period. Temperate males sang at higher rates when compared to subArctic males. Maintaining a high song rate while provisioning nestlings may be advantageous if a second brood is attempted. Our results suggest behavioral plasticity as a result of differing constraints on time and reproduction. *Received 3 April 2006. Accepted 28 August 2006.*

The Yellow Warbler (*Dendroica petechia*) has the broadest breeding distribution of any *Dendroica* species (Dunn and Garrett 1997, Lowther et al. 1999) and occurs in high density over much of its range (Sauer et al. 2001). This species' mating system is characterized by monogamy and biparental care, but extra-pair mating (Yezerinac and Weatherhead 1997, Yezerinac et al. 1999) and polygyny have been documented (Ford 1983, 1996; DellaSala 1986; Reid and Sealy 1986; Spector 1991). Such deviations from the typical mating system may occur mainly at lower latitudes, because the brief northern breeding season enforces increased nesting synchrony and reduces opportunities for extra-pair interactions when compared to more temperate populations (Briskie 1995, Yezerinac et al. 1999).

We earlier demonstrated that males breeding at high latitude display a significantly reduced endocrine response to stress during nestling provisioning (when compared to temperate-breeding males) to help optimize the tradeoff between individual risk and short-term reproductive success (Wilson and Holberton 2004). In the present study, we investigated whether corresponding behavioral plasticity occurs in the time- and energy-demanding behavior of singing. We predicted that subArctic-breeding males would spend less time singing during the nestling period when compared to their temperate counterparts, particularly late in the nestling period, when energetic demands of their growing nestlings are highest. Temperate-breeding males also have demanding nestlings during this stage, but we predicted they would be less constrained by parental care and more likely to continue defending territories and females in preparation for a possible second breeding attempt.

METHODS

We found Yellow Warbler nests along the Churchill River near Churchill, Manitoba (58° 37′ N, 94° 13′ W) in early June 1999, and in areas immediately around Jennings Randolph Lake (JRL; 39° 24′ N, 79° 07′ W) in Garrett County, Maryland and Mineral County, West Virginia in May 2000 and 2001. The male of each nest was captured after the onset of incubation by the female but prior to hatch of the eggs. Birds were marked with a USGS aluminum leg band and a unique combination of colored leg bands. The nestling period was divided *a priori* into early (days 1–3), middle (days 4–6), and late (days 7–9) stages. Each male's song rate (songs/hr) was expressed as the number of songs during focal, 1-hr-long observation periods on days 2, 5, and 8. Observations were conducted between 0500 and 0900 hrs CDT at Churchill and between 0700 and 1100 hrs EDT at JRL (within 1–4 hrs following sunrise at each location). Each color marked male was confirmed as the male of the

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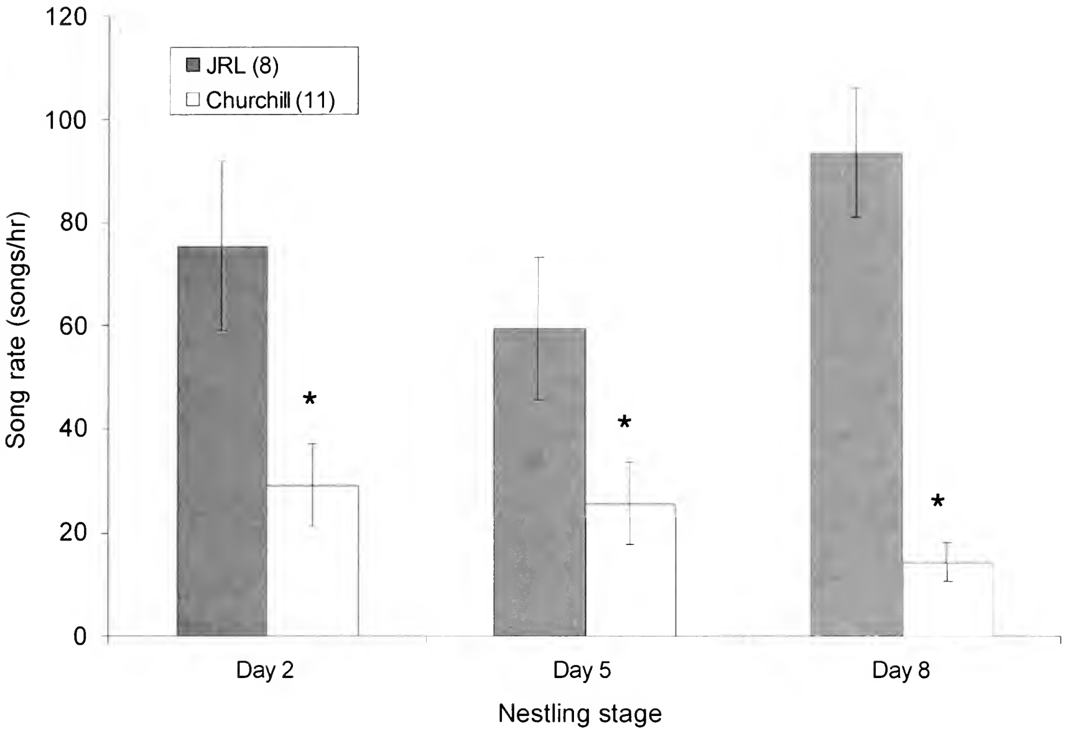

FIG. 1. Song rates of male Yellow Warblers during the nestling period were higher in a temperate study site (JRL; Maryland and West Virginia) than at a subArctic site (near Churchill, Manitoba) and did not change over the nestling period at each site. Sample size shown in parentheses. Bars represent the mean ± SE. An asterisk represents a significant difference ($P = 0.01$, 0.04, and < 0.001 for days 2, 5, and 8, respectively).

territory by observing him provisioning nestlings.

Seventeen or more nests were found at each study site, but only 11 (Churchill) and 8 (JRL) remained intact throughout the study period. Data were normally distributed and statistical analyses were performed using StatView version 4.51 (Abacus Concepts, Inc., Berkley, CA, USA). A single-factor repeated measures analysis of variance (ANOVA) was used to examine song rate at each site, with nestling stage comprising the repeated measure component. A two-factor repeated measure ANOVA was used to test for differences in song rate between the sites, with nestling stage comprising the repeated measure component. Fisher's protected least significant difference (PLSD) was used for *post hoc* analyses. Breeding density at each site was calculated by dividing the number of nests by the estimated total area of nesting habitat studied, using distinct habitat edges (e.g., water body and forest edges) to define this area.

RESULTS

The breeding density of Yellow Warblers at Churchill was almost three times as high as at JRL (~3.6 vs. ~1.3 pairs/ha). However, JRL males sang at higher ($F_{1,17} = 25.28$, $P < 0.001$) rates than did Churchill males overall and at each nestling stage (song rates ± SE on days 2, 5, and 8, respectively: JRL, 75.50 ± 16.51, 59.38 ± 13.82, 93.50 ± 12.47; Churchill, 29.18 ± 7.80, 25.64 ± 8.10, 14.36 ± 3.68; Fig. 1). There was a significant song rate × site interaction ($F_{2,17} = 3.64$, $P = 0.04$), but since song rates did not vary across the nestling period at either site (Churchill $F_{2,10} = 1.74$, $P = 0.10$; JRL: $F_{2,7} = 1.74$, $P = 0.21$; Fig. 1), this interaction may be a statistical artifact.

DISCUSSION

The higher breeding density of Yellow Warblers at Churchill might have been expected to lead to a high rate of singing behavior, but this was not the case; JRL males sang at much higher rates. The difference between sites may reflect differences in territory size, food availability, and/or other ecological factors, or differences between the subspecies that occur at the sites (*D. p. parkesi* and *D. p. aestiva*, respectively; Browning 1994). However, we suggest the difference may also reflect differences in breeding biology. Under harsh and/or unpredictable conditions, paternal care may be crucial to reproductive success (Bart and Tornes 1989, Lynn and Wingfield 2003). Thus, Churchill males may invest more in parental care and less in singing. Following brood-rearing (median hatch date at Churchill, 27 Jun), males must transition quickly from reproduction to molt to prepare for migration by mid August (Jehl 2004). Therefore, second broods are highly unlikely because of time constraints (Briskie 1995, Dunn and Garret 1997, Jehl 2004). In contrast, while paternal care may also be important to reproductive success in temperate populations, the higher song rate of temperate males may help maintain territories and retain mates if a second brood is attempted. The frequency of second broods in temperate populations of Yellow Warblers remains unclear, as they have been reported as both common (Dunn and Garrett 1997) and rare (Goossen and Sealy 1982). Second brood attempts were not studied at the JRL site. If attempted, the timing of the nesting cycle (median hatch date of 25 May) would likely result in a second clutch in mid to late June. Identifying the factor(s) that influence song rate in these two populations requires further study, but our results suggest behavioral plasticity of males of the same species faced with potentially different constraints on time and reproduction.

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Red-breasted Sapsuckers Nest in Utility Pole

Steven R. Helm[1]

ABSTRACT.—A pair of Red-breasted Sapsuckers (*Sphyrapicus ruber*) was observed nesting in an electric distribution, creosote-treated, wood utility pole in the Willamette Valley, Oregon during spring 2006. To the author's knowledge, this is the first published account of a sapsucker nesting in a utility pole. *Received 5 July 2006. Accepted 4 August 2006.*

A pair of Red-breasted Sapsuckers (*Sphyrapicus ruber*) was observed nesting in an electric distribution, creosote-treated, wood utility pole from 29 May through 4 June 2006 in the Willamette Valley, Clackamas County, Oregon (T2S, R1E, S28). The approximately 12-m tall pole was installed in 1969 and was heavily damaged. The nest hole was at a height of 3.0 m, while four similar sized nest holes and numerous non-nest excavations were evident higher on the pole. On 8 June 2006, an adult was found dead on the pole. The bird's leg had become tangled in fine, black, plastic netting material that was present in the nest cavity. Apparently, the bird could not free itself as it flew from the pole. It is unknown whether the netting was used by the pair as a nest liner or placed by someone to cause nest failure. Nestlings were heard at the time the adult was removed but perished, as the nest was abandoned by the other adult. Red-breasted Sapsuckers had nested in this pole for several consecutive years according to local residents.

The pole was along a lightly traveled road in a semi-rural area and the nest hole faced east, toward the road. Habitat in the vicinity of the pole was characterized by a vineyard and farm with Christmas trees and scattered orchard trees to the west and mature riparian mixed forest, along the Tualatin River, to the east. Branches of an approximately 25-m tall Douglas-fir (*Psuedotsuga menziesii*) contacted the west side of the pole.

Red-breasted Sapsuckers, although known to drum on utility poles (Bent 1939), typically excavate nest cavities in large snags or live trees with decayed interiors (Howell 1952, Joy 2000, Walters et al. 2002). Nests in western Oregon are associated with dense midstory and understory cover in close proximity to water (Nelson 1988). New nest cavities are excavated each year, often in the same tree used in previous years (Howell 1952), and eggs are deposited on fine wood chips that are retained in the cavity (Bent 1939). Other species of woodpeckers are known to nest in utility poles causing significant damage (Dennis 1964, Harness and Walters 2004). Lower nest success occurs in recently installed, treated poles compared to more weathered, older (15 to 20 years), treated poles (Rumsey 1970).

None of the four currently recognized species of sapsuckers (AOU 1998) has previously been reported, to the author's knowledge, to nest in utility poles. This account departs from published literature on nesting habitat of sapsuckers in general, and suggests that Red-breasted Sapsuckers are more opportunistic than previously thought. Photographic documentation of the nesting pair was submitted with the manuscript.

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The First Specimen Record of Gray Heron (*Ardea cinerea*) for North America

Martin Renner[1,3,4] and Paul D. Linegar[2]

ABSTRACT.—A Gray Heron (*Ardea cinerea*) was found alive on 11 October 1996 in Newfoundland, Canada. It was identified as a Great Blue Heron (*A. herodias*), and prepared as a study skin for a university teaching collection. We give a description of this first specimen for North America and summarize previous records from the western hemisphere. *Received 31 October 2005. Accepted 1 March 2006.*

The first Gray Heron (*Ardea cinerea*) specimen for North America was discovered by MR while selecting bird specimens from a teaching collection for an ornithology class at Memorial University of Newfoundland (MUN) in September 2002. It had been lying, misidentified, in the MUN collection for years. The bird has been found moribund on 11 October 1996 at Lear's Cove (46° 50′ N, 054° 11′ W), Avalon Peninsula, Newfoundland, about 3 km north of Cape St. Mary's and taken to Salmonier Nature Park where it died. This bird was presumed to be a Great Blue Heron (*Ardea herodias*), was frozen and sent to the Biology Department at MUN to be used in teaching specimen preparation. The skin was prepared by a student, deposited in the collection, and labeled as a Great Blue Heron. It is now deposited in the Royal Ontario Museum as catalog number ROM 104256: male, culmen: 120 mm, flattened wing: 455 mm, tarsus: 152 mm (measurements by MR).

DESCRIPTION AND IDENTIFICATION

The heron was gray above and white on the belly. The sides of the neck were uniform gray, and the crown was gray with a small blackish gray crest. The combination of a gray neck and white belly, and size rules out most of the world's herons other than Gray and Great Blue herons.

Plumage.—The specimen lacks any rusty brown on the leg feathers or on the underwing or neck in contrast to a Great Blue Heron. There is a slightly buffy hue on the thighs. The front of the neck is white with bold black spots of high contrast. Thinner, longer, less well-defined black streaks continue from the neck to the belly. The neck on the Gray Heron is plain gray laterally without such markings

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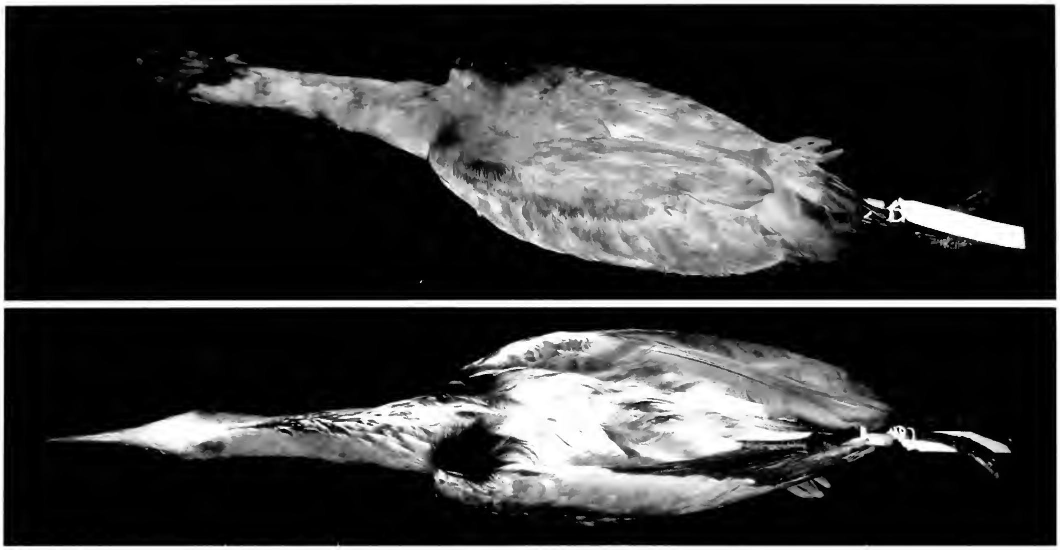

FIG. 1. Dorsal and ventral view of Gray Heron, found on 11 October 1996 at Lear's Cove, Newfoundland.

as the distinct pale streaking along the side of the neck of immature Great Blue Herons

Size and Proportions.—The Newfoundland Gray Heron was a male (based on dissection as noted on the specimen label). Herons show slight sexual dimorphism in size with some overlap (Butler 1992, Cramp and Snow 1998). The bill especially appears proportionately shorter in the Gray Heron (Figs. 1, 2). The culmen length of the Newfoundland specimen

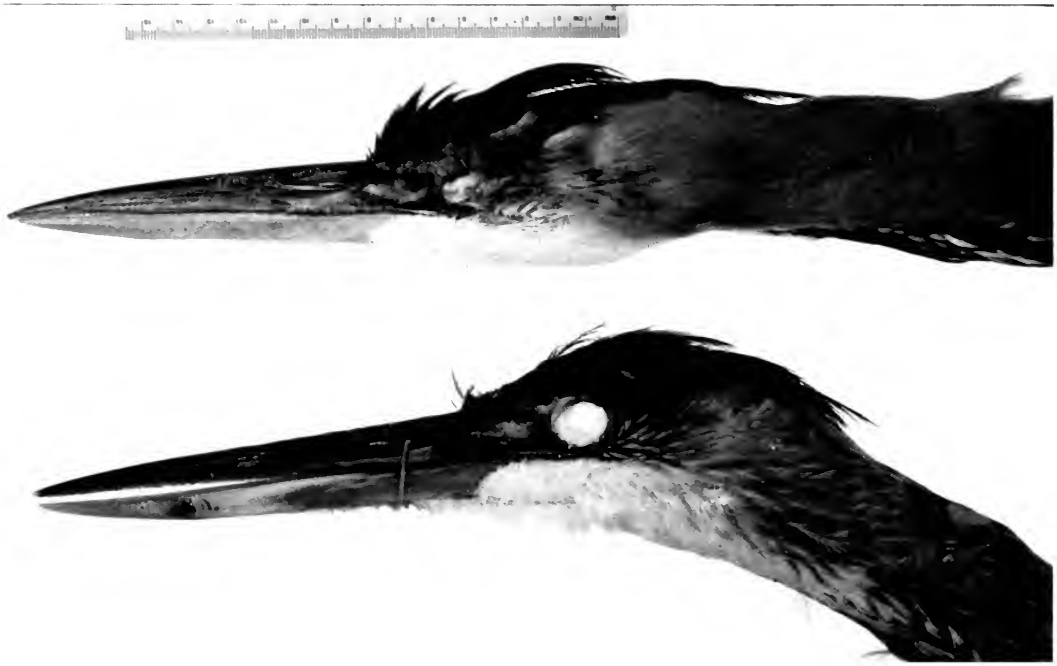

FIG. 2. Gray Heron (above) and Great Blue Heron (below) in the Memorial University of Newfoundland collection. Note difference in bill proportion and details in feathering.

is within the published range for Gray Heron but outside the expected range for Great Blue Heron.

DISCUSSION

The heron was picked up near Cape St. Mary's, which is close to the major shipping lane from Europe to the Gulf of St. Lawrence. Thus, partial ship assistance cannot be ruled out; however, there is no direct evidence to suggest the bird hitched a ride. Its emaciated condition is consistent with having flown at least a large proportion of the trip. The timing of this record matches the main migration season for the species in Europe (Sep–Oct) (Cramp and Snow 1998) as well as arrival of vagrants on Barbados (Oct–Nov) (Buckley et al. 2006). This bird was a 1st-year bird based on the blackish-gray crown, short nape-plume, and gray sides of the neck (Mullarney et al. 1999).

We know of no previous specimens from North America. Gray Herons wander widely, averaging about 50 sightings a year on Iceland in recent years (Shanahan 2001) and have been recorded at least 15 times in Greenland, mainly in fall (Boertmann 1994). In the Caribbean, Gray Herons have been found on Barbados (first recorded in 1963; year-round resident since 1997 with up to 5–6 birds simultaneously; Buckley et al. 2006), Montserrat, Martinique, Trinidad, and Tobago (Shanahan 2001). A bird banded as a nestling in France was shot the next year on Trinidad (Ffrench and Ffrench 1966). Banded birds have also been found on Montseratt (Baudouin-Bodin 1960) and Capitao Poco Ourém Pará, Brazil (Sick 1993:134). A Gray Heron was found dead on Bermuda on 7 October 2005 (Dobson 2005). There is also a sight record from Saint Paul Island, Alaska, which has been recorded as unsubstantiated (Burton and Smith 2001). A Gray Heron survived a trans-atlantic voyage on board a cargo vessel in 2002. Three Gray Herons landed on the ship northwest of the Azores on 26 September. One of them died and was discarded, another one died and the specimen was saved. The third bird was still alive when the vessel docked in Conception Bay on 3 October but died soon afterward in Salmonier Nature Park. One of the specimens is now in the Newfoundland and Labrador Museum, St. John's.

During most of October 1996, a broad high-pressure ridge prevailed over the North Atlantic between Newfoundland and Britain, resulting in westerly winds to the east of Newfoundland. However, on 10 and 11 October, two low-pressure systems, remnants of hurricane Josephine, created an easterly flow of winds from Iceland via Greenland to Newfoundland. If this heron did not ride on a ship, it could have ridden these winds from Iceland to Newfoundland.

ACKNOWLEDGMENTS

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Gang-brooding in Northern Bobwhites in West Texas

Jason L. Brooks[1,3,4] and Dale Rollins[2]

ABSTRACT.—We report the occurrence of gang-brooding (i.e., communal brood-rearing) in a population of Northern Bobwhites (*Colinus virginianus*) in western Texas. Combinations of adult quail (2 mated pairs, 2 males, and 2 females) were observed with broods on several occasions. During the two-year study (2003–2004), communal broods were documented only in summer 2003. *Received 3 April 2006. Accepted 25 September 2006.*

Northern Bobwhites (*Colinus virginianus*) have several reproductive strategies to enhance recruitment including large clutch size, multiple clutches, and male incubation (Burger et al. 1995). Faircloth et al. (2005) described four possible post-hatch brood amalgamations in bobwhites: adoption, creaching, gang-brooding, and kidnapping. Here we define gang-brooding as two or more broods combining with pairs or single adults. This differs from other post-hatching brood amalgamations involving only the adoption or mixing of offspring. Gang-brooding has been observed in other species of quail, including California Quail (*Callipepla californica*) (Lott and Mastrup 1999) and Gambel's Quail (*C. gambelii*) (Brown et al. 1998). Gang- brooding conferred survival and was adaptive in California quail; adult quail involved in communal brooding lived longer than adults not involved in communal brooding (Lott and Mastrup 1999). Gang-brooding has not been documented in Northern Bobwhites across the more arid parts of their range, e.g., Texas and Oklahoma, despite numerous studies dealing with radio-marked birds and nesting records (e.g., Burger et al 1995, DeMaso et al. 1997, Hernandez et al. 2003).

METHODS

We followed adult radio-marked bobwhites to monitor reproduction in southwestern Fisher County in the Rolling Plains Ecoregion of Texas during the 2003 and 2004 breeding seasons. The radio-marked individuals were located twice weekly by triangulation and once by walking in on the bird until a visual sighting was obtained (Brooks 2005). All reports of gang-broods were from visual observations of radio-marked birds. These observations commonly resulted in flushing of the adults and possibly the broods.

OBSERVATIONS

The first occurrence of gang-brooding involved two apparently unmated hens (only one of which was radio-marked) combining broods. The radio-marked hen hatched eight of nine eggs on 3 June 2003. Seven days post-hatch (10 Jun 2003) the hen was observed with another mature hen and >15 chicks. A similar observation occurred at 14 days post-hatch (17 Jun 2003). However, at 4 weeks post-hatch the radio-marked hen abandoned the brood, or left it in the care of the other hen. On 15 July the radio-marked hen was found incubating a second nest.

Two radio-marked males were responsible for the care of the second gang-brood. They were first observed on 7 July 2003 and the brood remained intact until radio failure prohibited further monitoring of the adult males on 1 August 2003.

The final gang-brood was reared by two (presumably) mated pairs, of which both females and one male were radiomarked. Both clutches were incubated by the radio-marked females and hatched on the same day (4 Jun 2003). The first observation of all birds together occurred on 1 July. This group of four adults and surviving chicks stayed intact until 15 August when the still-functioning radio transmitters were removed.

DISCUSSION

All three instances of communal broods were observed in 2003. Breeding activity of

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the radio-marked sample ceased on 28 July 2003 likely because of hot, dry conditions. Only 10 broods were produced by the adult sample in 2003. Rainfall was absent from 1 July to 28 August with daytime ambient temperatures routinely climbing above 35 °C. Heat can affect behavior and reproductive effort of Northern Bobwhites (Guthery 2002: 19). In 2004, weather conditions were more favorable and the sample population was actively engaged in nesting activities at the end of the study on 31 August.

Gang-brooding may allow bobwhites greater flexibility in reproductive behavior. Faircloth et al. (2005) estimated a range of 22–66% of broods had some form of post-hatch amalgamation at 10–12 days in Florida. Lott and Mastrup (1999) demonstrated that California Quail which raised communal broods lived longer and hatched more eggs. All chicks of the communal broods in our study were similar (within 1 week) in age. Proximity in age and location may be important for initiating combining of broods (Lott and Mastrup 1999). This behavior may be an adaptation to relatively short-lived optimal nesting conditions allowing them to invest maximally in chicks rather than multiple-clutch attempts. Scaled Quail (*Callipepla squamata*), which are endemic to the Chihuahuan desert, have been observed to hatch two broods per summer (Carter et al. 2002, Buntyn 2004) but no instances of gang-broods have been reported. Additional studies are needed to assess the frequency and possible environmental stimuli (e.g., hot, xeric conditions) that may predispose Northern Bobwhite to gang-brood their chicks.

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Once Upon a Time in American Ornithology

Elliot Coues was one of the 19th century's most scholarly and productive ornithologists. A lover of nature, an original thinker, and a "readable" scientist, Coues was often found writing at his desk "as if his life depended on it." Born in 1842 in New Hampshire, he graduated from college by the age of 19 and received his M.D. from the National Medical College, Washington, D.C. in 1863. He was commissioned as Assistant Surgeon in the U.S. Army in 1864 and spent the next 17 years in the Army as a medical officer at various posts. An Army Surgeon in name only, Coues was often given free reign to pursue his interest in ornithology, and was allowed to write about birds and collect specimens at will.

Coues' interest in birds began early in life. Shortly after the family moved to Washington, D.C. in 1853, Coues was befriended by Spencer Baird, an ornithologist with the Smithsonian Institution, who became Coues' primary mentor. One of the greatest influences on Coues' professional life was an early (1864) trip with an Army unit to the Southwest, arranged by Spencer Baird. Much of his time during that period was spent at Fort Whipple, Arizona, "a month's journey from anywhere," but an exceptionally eligible spot for collecting birds—many, as it turned out, new to science. Of his Arizona experience, Coues wrote: ". . . my enthusiasm runs so high that sometimes as I stand alone in the wilderness, thousands of miles from home and friends, hot, tired, dirty, breathless with pursuit, but holding in my hand and gloating over some new and rare bird, I feel a sort of charitable pity for the rest of the poor world, who are not ornithologists and have not the chance of pursuing the science in Arizona."

Much of Coues' professional life was dedicated to taxonomy, with numerous published works including his *Key to North American Birds,* published in 1872. Under the influence of Darwin's *On the Origin of Species* (published in 1859), Coues was always trying to answer what constitutes a species. For example, in a letter to J. A. Allen he writes: ". . . I do not know what a species is in the least, and that no one else is much better off in this respect than I am." Though instrumental in furthering the use of trinomial nomenclature, Coues was, in the end, a "lumper" and not a "splitter."

In his later years, Coues became a scholar of American history, and he was highly skilled as an editor. His travels in 1873–1874 along much of the route of the Lewis and Clark expedition, for example, led to papers comparing his scientific investigations with those of Lewis and Clark as well as appraisals of the technical results of their expedition. In later life, Coues edited "the Biddle edition"—the first account, published in 1814 by Nicholas Biddle—of the original journals of Lewis and Clark.

Notably, Coues also served as a counselor and mentor to bird portraitist Louis Agassiz Fuertes, and was instrumental in advancing Fuertes' career. In 1883, along with J. A. Allen and William Brewster, Coues conceived of and established the American Ornithologists' Union. Coues died of pneumonia on 25 December 1899 at the age of 57.

Known for his literate writing style and elegant life history accounts (*Birds of the Northwest,* 1874; *Birds of the Colorado Valley,* 1878), Coues' account of an experience with Sharp-tailed Grouse (*Tympanuchus phasianellus*) in 1872 is typical. Coues wrote the following narrative while stationed along the Missouri River at Fort Randall, Dakota Territory (in what is now Mix County, South Dakota), on another of his many tours of duty as Army Surgeon. The original reference is: Coues, Elliot. 1874. *Birds of the Northwest: A Handbook of the Ornithology of the Region Drained by the Missouri River and Its Tributaries.* U.S. Geological Survey of the Territories. Miscellaneous Publication 3. Washington, D.C.: Government Printing Office.—JAMES A. SEDGWICK; jim_sedgwick@usgs.gov

"I shall never forget the first time their strange booming fell upon my ears—a new experience to me. . . . I was miles away from the fort or any other human habitation, whither I had gone into lonely bivouac the night before. . . . Awakened before it was light by the sonorous cries of the wild fowl making for the reedy lake where I had encamped, I arose . . . and pushed off into the expanse of reeds in a light canoe I had brought with me. . . . The sense of loneliness was oppressive in the stillness that preceded morning, broken only by the quack or plash of the Wild Duck, and the distant honking of a train of Wild Geese winnowing their sinuous way afar. . . . The light came on, the distant hills took shape and settled in firm gray outlines against the sky, and a breath of fresher, purer air, messenger of morning, passed over the lake . . . causing the reeds to sway in graceful salute to the coming sun. A Sparrow chirped from her perch with joy; a Field Lark rose from her bed in the grass. . . . The feathered orchestra sounds never so impressive as when it ushers in the day; never so fine and complete as when familiar voices sing the higher notes to the strange deep bass of the [Sharp-tailed] Grouse. Heard for the first time, as it was on this occasion, the effect was indescribable. No one could say whence the sound proceeded, nor how many birds, if more than one, produced it; the hollow reverberations filled the air, more like the lessening echoes of some great instrument far away, than the voice of a bird close at hand. I listened to this grand concert, absorbed in the reflections it stirred within me, no longer alone, but in company I love, till the booming fell less frequently upon my ear, and then ceased."

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Ornithological Literature

RAPTORS OF THE WORLD: A FIELD GUIDE. By James Ferguson-Lees and David Christie. Princeton University Press, Princeton, New Jersey, USA. 2005: 320 pp., 16 figs., 118 plates, and 7 tables. ISBN: 13-978-0-691-12684-5. $29.95 (paper).—This new "field guide" to the vultures, hawks, eagles, and falcons of the world represents a distillation of the earlier "identification sections" of the handbook-sized, *Raptors of the World,* by the same authors (Houghton Mifflin, 2001). One hundred and eighteen color plates by Kim Franklin, David Meade, Philip Burton, and Alan Harris illustrate 338 species of raptors, perched and in flight. There are 77 pages of useful introductory materials, including a list of all species and subspecies, together with information on raptor identification, raptor migration, molt, taxonomy, and English names. The first three plates offer keys to the genera of small, medium, and large raptors. The remaining 115 plates are arranged taxonomically and—within taxa—regionally (e.g., island-endemic, Neotropic, Nearctic, and Palearctic buteos, etc.).

In spite of recent and much needed DNA analyses of the "group," the taxonomy of diurnal birds of prey remains somewhat confused and in considerable dispute. *Raptors of the World: a field guide* adopts an inclusive and species-splitting approach. The recently rejoined New World Vultures begin the work, and 24 forms treated as subspecies in the earlier handbook are considered full species in the field guide. A recently discovered *Micrastur* also is included.

The heart and soul of any field guide rests in its ability to help readers identify birds in the field. *Raptors of the World: a field guide* does so admirably, particularly for species from parts of the world where regional field guides for raptors have yet to be published (i.e., places other than North America, Europe, the Middle East, South Africa, and Australia). Indeed, when Ferguson-Lees and Christie published their handbook in 2001 I immediately bought two copies: one for my office and one for the field; with the latter being split and rebound into separate text and plate volumes.

I have since used the plates most extensively in Central and South America, but they also have served me well as a supplement to existing regional guides for Europe and the Middle East. Compared with recent regional guides, the new "world guide" comes up short in several expected ways. First, regional guides are not "cluttered" with look-alike species from other areas, which can make finding the images in *Raptors of the World: a field guide* difficult. Second, regional guides spend considerably more time and space on each species and, typically, offer more information about each of their subjects. Third, regional guides, which are written by regional experts, often capture a species field marks and "jizz" better than Ferguson-Lees and Christie. For these reasons, I recommend using the current work as a back-up to regional guides whenever the latter are available. That said, *Raptors of the World: a field guide* provides the best source of portable information available for Neotropic, Eastern Palearctic, Central African, and island raptors, and in these parts of the world the new guide is an essential tool for anyone serious about identifying raptors in the field.

As is true of any field guide illustrated by more than one artist, one can easily quibble about unevenness in the plates, and certainly some of the images stand out as far better than others. That said, almost all of the illustrations are superior to those available in most general bird guides, particularly for areas outside of North America, Europe, and other well-birded regions. One useful feature of several of the plates is the depiction of specific behavioral patterns useful in field identification. The Crane Hawk (*Geranospiza caerulescens*), for example, is shown thrusting its foot into a nest cavity in search of prey, and a flock of Chimango Caracaras (*Milvago chimango*) is shown following a plow. Many other species are illustrated with typical prey in their talons.

The text that accompanies the plates, while adequate and easy to follow, begs for the inclusion of a section on "similar species" for each account. Although the 152-by-228 mm (6-by-9-inch) format makes the work larger than a typical pocket field guide, the book's production and binding appear to be first rate.

Raptors of the World: a field guide is far and away the closest thing to a perfect world guide for birds of prey available, and should be on the shelf and in the backpack of raptor aficionados everywhere. I will be taking my copy into the field for years to come. I highly recommend this innovative and useful guide to anyone interested in identifying and learning more about birds of prey.—KEITH L. BILDSTEIN, Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, 4120 Summer Valley Road, Orwigsburg, Pennsylvania; e-mail: Bildstein@hawkmtn.org

THE BIRDS OF SÃO TOMÉ AND PRÍNCIPE WITH ANNOBON ISLANDS OF THE GULF OF GUINEA. BOU Checklist No. 22. By Peter Jones and Alan Tye. British Ornithologists' Union/British Ornithologists' Club, Oxford, United Kingdom. 2006: 172 pp., 34 plates, 8 maps. ISBN: 0-907446-27-2. Price £30 (cloth).—This latest volume in a steadily lengthening line of worthy checklists produced by the British Ornithologists' Union focuses on a chain of small, remote and until recently almost forgotten volcanic islands that straddle the equator off of the coast of Western Africa in the Gulf of Guinea namely Príncipe, São Tomé, and Annobon. Discovering and rediscovering the avian secrets of these islands has been the objective of a number of intermittent and variously successful ornithological expeditions since 1800 and, indeed, only recently have several supposedly 'lost' species come to light. The high number of endemic species relative to land mass on these islands has attracted the attention of collectors, taxonomists, and more recently visiting birdwatchers.

The islands of São Tomé and Príncipe, in particular, have become easily accessible with regular connecting international flights and are now firmly on the birding map for tourists and birders eager to add some fascinating and rare endemic species to their world lists. Thus, this book is a useful tool for any prospective visitor. Oddities to be found include the once almost mythical São Tomé Grosbeak (*Neospiza concolor*), a unique forest dwelling Fiscal (*Lanius newtoni*), the strange Dohrn's Thrush Babbler (*Horizorhinus dohrni*) for which a tag of *incertae sedis* is certainly well applied, the world's largest Sunbird (*Dreptes thomensis*), the Weaver (*Ploceus grandis*), and the Dwarf Olive Ibis (*Bostrychia bocagei*).

The authors were responsible for an ICBP study report published in 1988 of the islands of São Tomé and Príncipe based on a five weeks visit to the islands. This personal experience has been combined with a thorough review of the scientific literature available. A concise and readable introduction outlines the geography, history, geology, and climate. Trends in breeding, migration, and the origins of the avifauna are discussed, and a brief summary of the other endemic fauna and flora is given. The nomenclature follows *Birds of Africa,* while the taxonomy used tends to follow a middle road, being influenced by Naurois, Collar and Stuart, Sibley and Monroe, and Dowsett and Dowsett-Lemaire. The authors recognise 28 endemics, 6 solely on Príncipe, 15 on São Tomé and 2 on Annobon. Four others occur on both Príncipe and São Tomé with another one shared by all three islands. There is a summary checklist, extensive gazetteer, and bibliography. A selection of pleasing color photographs illustrate the habitats of the three islands.

Most of the book is taken up with species accounts and historical records for the islands are summarised up to 1997. Alternative Portuguese and Spanish names are listed followed by referenced summaries on distribution, abundance, status, migrations, habitat, behaviour, breeding, and threats. The list errs on the side of caution regarding sight records and most of those not substantiated by their presence in collections demand the need "for confirmation" from the authors. Thus, the list provides a solid basis that will surely be the essential reference for future records but also allows much scope for new discoveries particularly concerning migrants and the seabird population where there is obviously still much to be learned. One of the strangest omissions is that regarding the section on vocalisations; it seems exceedingly odd that no reference is given in either the text or bibliography to the set of recordings of West African birds compiled by Claude Chappuis, which admirably include the vocalisations of most of the species to be encountered on the islands. By listening to these recordings one would immediately realise that the São Tomé Fiscal is certainly not "rather silent" for its cries can be loud and constant thus drawing attention to its presence. During a recent 'Birdquest' trip to São Tomé we could hear three separate individuals calling at the same time from different directions; their far-reaching calls must help in setting up territories in the steep, forested valleys. My own personal observations can also confirm that Lemon Doves (*Columba larvata*) on São Tomé definitely are found feeding on the roads along with Laughing Doves (*Streptopelia senegalensis*) and that white phase Western Reef Egrets (*Egretta gularis*) are certainly not absent on Príncipe.

The taxonomic position of many species of the islands is perhaps one of the most interesting aspects of the book and although some species are discussed, regrettably others such as Lemon Dove, Blue-breasted Kingfisher (*Halcyon malimbica*), Gulf of Guinea Thrush (*Turdus olivaceofuscus*), and Chestnut-winged Starling (*Onychognathus fulgidus*) have been ignored completely. One quibble with the choice of English names involves *Ploceus velatus* that the authors choose to call Vitelline Masked Weaver. This name is more appropriately given to the form *vitellinus* usually treated as a separate species. Either African or Southern Masked Weaver as used in *Birds of Africa* would have been more apt. On an aesthetic level, I wonder why the book could not have included some color plates depicting the endemic species and it is a pity the main picture of Dohrn's Thrush Babbler on the cover shows the bird in a totally uncharacteristic pose! My review copy had the first 50 pages damaged by deep creases, so prospective Internet or postal buyers beware! These minor issues aside, this is undoubtedly a well-researched investigation into the state of the current understanding of the avifauna of the island and will obviously act as an important benchmark for the decades to come.—NIK BORROW, London, United Kingdom; e-mail: n.borrow@btinternet.com

THE BIRDS OF ANGOLA. BOU Checklist No. 18. By W. R. J. Dean. British Ornithologist's Union, Tring, Hertfordshire, United Kingdom. 2000: 433 pp., 10 tables, 9 figures, 33 plates, 9 distribution maps. ISBN: 0-907446-22-1. GBP 50.00 (cloth)—The *Birds of Angola* is part of the new series of BOU Checklists and follows the format of the previous titles living up to the high standard of proof reading we expect from the BOU. Angola remains poorly known and it must have been difficult to collate the data scattered in obscure collections and museums. The author summarizes all collections and expeditions to date, noting that since the start of the civil war in 1974 all studies stopped. Not a single Angolan bird has been studied in depth in country, making an atlas impossible as so little is known of the distribution. Data on breeding birds were minimal at the time of publication and it is only since 2005 that a few ornithologists have again been visiting the country. Knowledge of the status and distribution of most of the almost unknown 10 endemics, which are briefly detailed in the book, is now at last increasing.

The introductory chapters detail the geomorphology and geology, climate, vegetation zones and zoogeography, and migration and breeding with a section on conservation which is again receiving some attention after Angola's years of chaos. The vegetation zones are well described with a summary of characteristic species, including such enticing Afromontane relicts as Angola Cave-Chat (*Xenocopsychus lyalli*) and Swierstra's Francolin (*Francolinius swierstrai*). The Cabinda exclave has a large component of Guinea Forest species, many of which also occur in the north of Angola proper in Cuanza Norte and Cuanza Sul. The interior plateau has huge tracts of *Brachystegia* (miombo) woodland, while the Escarpment Zone has some of the least known endemics including Pultizer's Longbill (*Macrosphenus pulitzeri*) and Red-crested Turaco (*Tauraco erythrolophus*).

It would have been nice to have some plates of the endemic birds, but all we get is a painting of the Red-crested Turaco on the front cover. There are 33 color plates of habitats, some of which seem to largely duplicate each other, perhaps not the wisest marketing ploy.

The taxonomic sequence, taxonomy, and

vernacular names follow those of *Birds of Africa,* now beginning to show its age with the earlier volumes, although much better with the later ones. Status codes follow the usual BOU format with clear abbreviations such as RB for resident breeder. A critical eye has been cast over some of the early records of Traylor (1963), and those rejected are listed in square brackets in the text.

An introductory short paragraph summarises the distribution and status of each species, the latter given in general terms, with those of conservation concern duly identified although, oddly, the Angolan endemics are not actually mentioned as such in the relevant species text. Details of collected specimens are given where available from the literature and these form a large part of many of the species accounts; a list of where the specimens are located is given in abbreviated format.

A series of appendices give mean annual rainfall and dry season months at many localities in Angola, a tabular habitat analysis of Angolan avian families, ringing recoveries in Angola [mostly Cape Gannet (*Sula capensis*) and terns (*Sterna* spp.)], mass measurements in grams of Angolan birds, a comprehensive gazetteer, and a thorough list of references pertaining to Angolan birds. An index is given for scientific names and also for English and Portuguese names.

The book is a welcome addition to the literature on African birds dealing with one of the most poorly covered countries. It fits admirably into the BOU checklist series and is a valuable summary of information up to the mid 1990s. Hopefully, the recent political settlements in Angola will usher in an era of reconstruction and development, and some of the more obvious gaps in our knowledge, as shown by this book, can begin to be filled, as intrepid scientists and birders again visit that country. This book is recommended for anyone visiting or interested in this little known area.—PHIL GREGORY, Cassowary House, P. O. Box 387, Kuranda, Queensland 4881, Australia; e-mail:
sicklebill@optusnet.com.au.

THE BIRD ATLAS OF UGANDA. By Margaret Carswell, Derek Pomeroy, Jake Reynolds, and Herbert Tushabe. British Ornithologists Club/British Ornithologists Union, University of Oxford, United Kingdom. 2005: 553 pp., 11 tables, 10 text figures, 822 maps. ISBN: 0-9522866-4-8. GBP 55.00 (hardback).—*The Bird Atlas of Uganda* covers all species known to have occurred in the country up to the end of 1999, with pre-1990 records allocated where practicable to quarter square degrees, and post 1990 records presented on a point basis, with most assigned to the nearest kilometer. The first published data included is from 1891 and an exhaustive search of the literature was undertaken to make the atlas as comprehensive as possible. Less than 80 people contributed to the project, a small number in the context of such an undertaking and a major achievement when one considers the background and location of the work. Over 41,000 point records are detailed in the maps, which are given for all species with five or more records. Uganda becomes the 16th African country to have an atlas produced, (although six countries are included within the massive Southern African Bird Atlas).

The English names wisely follow the exemplary Stevenson and Fanshawe 2002 Field Guide, which will be the default reference work for a long time, and neatly avoids the pitfall of arbitrary names imposed from outside. Taxonomy is based on *Birds of Africa* but with up-dates from more recent authors such as Zimmerman et al. (1996), although a few odd things are unfortunately lumped such as African Scops Owl (*Otus senegalensis*) with Common Scops Owl (*O. scops*).

The introductory chapters by Derek Pomeroy are models of concision, the first section neatly summarising land–forms and past climates, the climate today, the still poorly understood phenomenon of seasonality, major ecological zones, bird habitats, human impacts on the natural environment and people and birds. The concept of Ecofloristic Zones (EFZ's), adopted for most of the work, uses a wide range of ecological criteria, which can help explain some seeming anomalies in distribution, such as the curiously local occurrence of Foxy Cisticola (*Cisticola troglodytes*). Most intact forest cover is within protected areas, and most areas have at least relics of the former habitat present, which helps explain the still great diversity of species in such a comparatively small country.

The end papers have maps of basic geographic features and both the old and current administrative districts. Maps in the introductory chapters clearly show altitudinal zones, rainfall, ecofloristic zones, vegetation type, land cover category, human population density, major protected areas and point coverage. The appendices present additions to the Ugandan list since January 2000, species whose occurrence is poorly documented, species whose occurrence is considered to be erroneous, and estimates of bird populations for a few species such as the iconic Shoebill (*Balaeaniceps rex*) which has 1–200 pairs. An extensive gazetteer and a comprehensive list of references and bibliography are provided, as well as a thorough index.

A brief history of ornithology in Uganda is given, referring to the classic work of Jackson and Sclater (1938), acknowledging the pioneering work of the East Africa and Uganda Natural History Society with its invaluable journal *Scopus* (inaugurated in 1977), and not forgetting the estimable Mackworth-Praed and Grant (1952, 1955) and *Birds of Africa* from 1982 onwards. The political and social stability which has followed the chaos of the 1970s has allowed the commencement of biodiversity surveys and work by professional ornithologists, culminating in the production of this landmark atlas.

The Atlas documents Uganda having 1,007 species of birds at the beginning of 2000 with a further 32 requiring confirmation. There is a valuable appendix detailing additional species whose occurrence is now considered erroneous. The only African countries with more species are Kenya, Tanzania, and the Democratic Republic of Congo (Zaire) with Tanzania having fewer breeding species. The numbers are in a similar league to the richest ornithological countries of South America.

About 190 species are regular migrants, mostly from the Palearctic, but more than 50 are intra-African migrants and many species exhibit partial migration, a phenomenon still poorly understood. Ringing (banding) has been conducted since 1950 but with only about 150 recoveries, so much remains to be learned about both movements and longevity. More than 80% of Uganda's birds are resident, but ~160 species lack breeding data including some surprisingly common ones including the Emerald-spotted Wood-dove (*Turtur chalcospilos*) and Greater Blue-eared Starling (*Lamprotornis chalybaeus*).

Over 300 of Uganda's birds are dependent on forest and 73 are Threatened according to regional and global extinction criteria with a further 118 listed as regionally Near-Threatened or of Regional Responsibility (i.e., predominantly East African in range). Forest cover has declined from an estimated 14% in 1900 to ~3.6% in 2000. Substantial areas of forest are now protected in reserves or parks but wetlands in particular face serious threats.

The atlas does not map breeding records because they are too few and mostly older data. What information is known is included within the text for each species, although only ~50 species have adequate breeding season data. The other residents are assumed to breed and the code 'RB?' (resident breeder) is used for their status; similar codes are being used by the BOU Checklist series. Each map is accompanied by a succinct and informative paragraph by Margaret Carswell, which gives estimates of status, comments on the distribution and subspecies involved, and lists what is known of the breeding cycle. There are also a few attractive black and white vignettes of birds.

An innovative feature of this work is the use of a predictive map model, developed and implemented by Jake Reynolds and Herbert Tushabe, that was derived from habitat suitability based on rainfall and vegetation type. This model delimits potentially suitable areas where the species may occur (exclusive of waterbirds which are outside the parameters of the testing). Some 498 of 822 mapped species get this treatment, basically the more widespread and often better known species. Given the lack of point data for such large areas of the country, especially in the north and east, this is a useful extrapolation and can be refined over time as better data become available. It may also have a considerable conservation value, helping identify potential key areas. Uganda contains parts of 3 Endemic Bird Areas (EBA's) and has 3 further secondary areas which harbor single restricted range species such as Lake Mburo National Park for Red-faced Barbet (*Lybius rubrifacies*) and

North Ugandan swamps for the sole Ugandan endemic, Fox's Weaver (*Ploceus spekeoides*). Uganda also has 30 Important Bird Areas (IBA's) identified with all 10 national parks qualifying for this status, plus 7 Forest Reserves and 2 Wetland Reserves. Efforts are under way to enlist the support of local people for formal protection for the 10 IBAs without protection.

The atlas highlights distribution changes via informative tables drawing attention to declines in fish-eating birds such as Pink-backed Pelican (*Pelecanus rufescens*) and Fish-eagle (*Haliaeetus vocifer*), and to worrying declines in Palearctic migrants, particularly the less common species such as Isabelline Shrike (*Lanius isabellinus*). This is a disturbing trend worthy of careful future monitoring. Increases have involved largely commensal species which can exploit degraded habitats, for instance the Marabou (*Leptoptilos crumeniferus*) is a recent colonist of Kampala!

The atlas is an innovative milestone for East African ornithology, provides a great baseline for future work and neatly summarizes the status of each species. Given the social and political problems which Uganda has so recently faced, it is a remarkable achievement, and gives invaluable data for conservation purposes. Given the current demographic explosion, careful planning and protection of key sites is vital and this work will be an exceptional resource tool. The authors are congratulated and every library or birder with African interests should possess a copy of this book.—Highly recommended.—PHIL GREGORY, Cassowary House, P. O. Box 387, Kuranda, Queensland 4881, Australia; e-mail: sicklebill@optusnet.com.au

CAPTIVE RAPTOR MANAGEMENT AND REHABILITATION. By Richard Naisbitt and Peter Holz. Hancock House, Surry, British Columbia, Canada. 2004: 168 pp., 107 color photographs, 11 black and white photographs, 80 line drawings and sketches. ISBN: 0-88839-490-X. $39.95 (hardbound).—Located at the migratory bottleneck at Eilat, Israel, at the northern edge of the combined North African deserts of the Sahel, Sahara, and Sinai, I have to contend with several 10s of raptors every spring that have succeeded to make the crossing successfully but that are too emaciated to go any further or blunder into human structures. During spring migration we are called on a daily basis to the tall hotels and the highest buildings to collect birds found by caring citizens and which have a wide range of injuries. The lack of a proper veterinarian in a radius of several 100s of kilometers has forced the staff of the International Birding & Research Centre in Eilat to rehabilitate as many as 300 raptors a season with absolutely no help from the outside. This has forced the dedicated staff to rely heavily on their own experience, gained by trial-and-error in the field, and books published on how to do it right.

There are several good books on the market that address the subject appropriately. However, the problems with them are that they are either too costly for a hand-to-mouth NGO, or are too technical for field use. Hence, I was skeptical when asked to review a copy of this book. It has taken more than one year to review the book because I decided to first use it in the field and to see how practical and useful it really might be.

The book is large, 85-by-110 mm, and hardbound. I found this to be an advantage in the field, especially on windy days. The writing is large and the illustrations are clean and clear. There are several 'boxed' tips and information that make the work easier for the person handling the bird. An example is on page 26 where there are checklists for when you initially receive the raptor—how to check for obvious injuries, what one should look for, and the proper procedures for examining the raptor. However, the book has two distinct sections that are inter-mingled.

Chapter one introduces the reader to the basics of raptor foraging ecology. This gives those who are not familiar with raptor ecology an idea of their functional capabilities. Chapter two dives into the subject of the injured raptor—how to collect and transport, housing, rehabilitation, and aviary exercise. This chapter also address the problems of dealing with orphaned raptors, their food, behavioral development, and re-introduction. Chapter three is dedicated to releasing rehabilitated raptors and chapter four to monitoring them after release. I found the section reviewing injuries especially useful, and built an aviary to exercise rehabilitated birds based on the recommendations. It has worked well for more than 100 raptors in the past 6 months.

Chapter five is important if there are any raptors that need care for extended periods of time. The chapter deals with beak and feather care, and housing of raptors. Chapter eight deals with raptor medicine and addresses soft-tissue and orthopedic injuries, ocular trauma, poisoning, and a variety of other problems. Chapter nine deals with the dietary requirements and the recommended body mass for several dozens of species of diurnal and nocturnal raptors.

In chapters 6, 7, and 10 the book takes a turn I was not expecting—it becomes a guide to basic falconry. This is a pity because the same publisher has covered falconry extensively in many other books and here is an add-on that has spoiled the effect of caring for wildlife that was broadcast in the other chapters.

On the whole, we found this book to be instructive in identifying problems with raptors brought to our center. This book will be good for beginning falconers and those who deal with wild raptor rehabilitation in places around the globe where veterinarians are a luxury and a lot of the work has to be done by the layman or field biologist.—REUVEN YOSEF, Director, International Birding & Research Center—Eilat, P. O. Box 774, Eilat 88106, Israel; e-mail: ryosef@eilatcity.co.il

The Wilson Journal of Ornithology 119(1):148, 2007

Editorial Comments

Clait E. Braun, Editor, 2007

Transitions between editorial offices are rarely smooth as some overlap may occur in assigning referees to manuscripts, duplication of manuscript assignment coding, changes in preferences, and editorial decisions. We are pleased the overall transition from the editing office in Fort Collins, Colorado to that in Tucson, Arizona starting in July 2006 has gone with few glitches. We appreciate the patience of referees and authors during this process which is mostly complete. We also greatly appreciate the support provided by Dr. James A. Sedgwick and his staff during the transition period.

The Tucson office has been functioning since early July with a staff of an editorial assistant (Nancy J. K. Braun) and myself. Eighty new manuscripts have been received since 1 July and we anticipate the total new manuscripts received in 2006 will exceed 170. We anticipate publishing between 80 and 100 manuscripts each year, suggesting there may be a rejection rate of ~40–50%. We are using electronic methodology as much as possible which speeds up manuscript review, routine correspondence with authors, and final editing. One manuscript was sent to and returned by referees, edited, and accepted within one month of original receipt. Decisions on other manuscripts (including the review process) have been made in less than 2 months. The largest delays are in the review process and in responsiveness of authors in returning their revised manuscripts. We have formed a list of possible referees by subject area and are constantly adding to it. Referees who can provide timely reviews within 3 weeks are in demand. Please contact us (TwilsonJO@comcast.net) if you wish to be considered as a referee.

We are also seeking to attract several Associate Editors for specific subject areas (Central and South America, avian use of habitats). This is an excellent way to learn more about the editing process, contribute to publishing ornithological studies, keep current on research in ornithology, and develop skills useful as an editor. An Associate Editor should be prepared to be responsible for up to 30 new different manuscripts each year. This may result in up to 10 hours of work each week in soliciting reviewers, reminding reviewers, conducting the initial edits of a manuscript, correspondence with authors, and making recommendations to the editor.

Editing is not for the timid as decisions are necessary. It is important to be considerate of authors, supportive of reviewers, and encouraging to those with useful data but with presentations that lack proper analysis and clarity. Referees and editors are human and may not be correct in their suggestions and overall perspective. Our goal is to fairly treat every manuscript received and to consider well-prepared rebuttals.

We appreciate the continuing support of the officers and elected council members of the Wilson Ornithological Society, authors for submitting their important manuscripts to the *Wilson Journal of Ornithology,* and especially, to those dedicated people who serve as referees and make the peer review process work. Our goal is to continue publishing the *Wilson Journal of Ornithology* on schedule (March, June, September, and December).

THE WILSON JOURNAL OF ORNITHOLOGY

GUIDELINES FOR AUTHORS

Please consult the detailed "Guidelines for Authors" found on the Wilson Ornithological Society Web site (http://www.ummz.lsa.umich.edu/birds/wilsonbull.html). Beginning in 2007, Clait E. Braun became the editor of *The Wilson Journal of Ornithology*. All manuscript submissions and revisions should be sent to Clait E. Braun, Editor, *The Wilson Journal of Ornithology*, 5572 North Ventana Vista Road, Tucson, AZ 85750-7204, USA. *The Wilson Journal of Ornithology* office and fax telephone number are (520) 529-0365. The e-mail address is TWilsonJO@comcast.net.

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The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution. The fund will be administered by the Library Committee. Robert Payne, University of Michigan, is Chairman of the Committee. The Library currently receives over 200 periodicals as gifts and in exchange for *The Wilson Journal of Ornithology*. For information on the Library and our holdings, see the Society's web page at http://www.ummz.lsa.umich.edu/birds/wilsonbull.html. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: Josselyn Van Tyne Memorial Library, Museum of Zoology, The University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA. Contributions to the New Book Fund should be sent to the Treasurer.

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Continued from outside back cover

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 119, Number 1

CONTENTS

March 2007

MAJOR ARTICLES

SHORT COMMUNICATIONS

Continued on inside back cover

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COVER: Wilson's Storm-Petrel (*Oceanites oceanicus*). Illustration by Don Radovich.

FRONTISPIECE. Male and female Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) tending to a nest. Smith et al. (page 151) found that heavy cutting forestry practices in southern Ontario, Canada create woodlots which favor the nest site preferences of Rose-breasted Grosbeaks. These woodlots may act as ecological traps by creating preferred nest sites yet resulting in lower nest survival and higher parasitism rates. Original painting (water color on paper) by Peter Burke.

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NEST-SITE SELECTION OF ROSE-BREASTED GROSBEAKS IN SOUTHERN ONTARIO

LYNDSAY A. SMITH,[1,2,5] ERICA NOL,[3] DAWN M. BURKE,[4] AND KEN A. ELLIOTT[4]

ABSTRACT.—Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) commonly breed in the deciduous woodlands of southern Ontario, but have become a species of conservation concern due to recent population declines (2% per year in Ontario from 1966 to 2004). We investigated whether habitat alterations may be contributing to these declines through decreases in nest survival at nest and randomly selected sites in 23 woodlots varying in the intensity of partial harvest. Rose-breasted Grosbeaks consistently selected nest sites with more sapling cover, less canopy cover, and a lower surrounding basal area than available. The best supported model of daily nest survival included a measure of nest concealment, with the top 15 models containing nest concealment indicating higher nest survival rates at less concealed nests. Model-averaged estimates produced positive slopes for canopy cover, sapling cover, and nest height indicating higher survival at higher canopy cover, sapling cover, and nest height. Heavy-cutting practices appear to create woodlots that act as ecological traps. These woodlots provide "preferred" nest sites that result in low nest survival probabilities for the Rose-breasted Grosbeak.

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Silvicultural practices alter the vegetative composition and structure of woodlots by removing trees of a variety of diameter classes and stimulating regeneration which affects bird communities and their demographics (Marzluff et al. 2000, Easton and Martin 2002). Bird communities should respond to this alteration in stand structure because of the direct impact it can have on the diversity and abundance of critical nest-site features (Rodewald and Smith 1998, Kingsley and Nol 1999, Yahner 2000). Forest stands naturally consist of several layers of vegetation, including herbaceous plants, shrubs and understory, and midstory and overstory trees, all of which provide structural diversity important for many bird species (Marzluff et al. 2000).

Most forests in the fragmented landscape of southern Ontario are periodically partially harvested. Landowners conduct either diameter-limit cuts where most of the largest trees are

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removed, or use prescriptions based on the single-tree selection silvicultural system. This system preserves a diverse stand structure while allowing for smaller volume harvests at shorter intervals (every 8 to 25 years; Ontario Ministry of Natural Resources 2000). Changes in forest structure and composition based on different harvesting intensities influence the availability of nest sites for forest breeding songbirds. When forest songbirds select nest sites, they use vegetation structure as a proximate cue, which is ultimately tied to protection from predators (Sallabanks et al. 2000, Easton and Martin 2002). Thus, decisions about nest placement should be influenced by nest-site characteristics that minimize risks of predation and parasitism (Martin and Roper 1988, Martin 1998). Many studies have examined the effect of nest-site habitat variables on avian nest survival (Powell and Steidl 2000, Ricketts and Ritchison 2000, Nguyen et al. 2004, Vergara and Simonetti 2004), although few have found habitat variables that confer higher nest success (Martin and Roper 1988, Liebezeit and George 2002).

The Rose-breasted Grosbeak (*Pheucticus ludovicianus*) is a common forest bird, but little is known of its nest-site selection (Peck and James 1987, Burke 1998, Wyatt and Francis 2002). Populations in Ontario, Canada declined at a rate of 2% annually during 1966 to 2004 (Sauer et al. 2004). Their nest-site microhabitat is characterized by open canopy and sub-canopy, with deciduous saplings selected as nest foundations more often than tall trees (Peck and James 1987, Wyatt and Francis 2002). Nest-site selection appears unrelated to shrub cover, sapling cover, or ground cover within a 5-m radius of the nest (Wyatt and Francis 2002). We designed our study to: (1) identify nest-site microhabitat used by breeding Rose-breasted Grosbeaks, (2) investigate whether partial harvesting alters nest-site selection parameters, (3) examine whether preferred microhabitat features influence rates of daily nest survival or nest parasitism, and (4) relate how changes in nest-site microhabitat—driven by harvest-related changes in vegetation structure and composition—influence the demography of Rose-breasted Grosbeaks.

METHODS

Study Area.—We surveyed 23 woodlots (Fig. 1) in southwestern Ontario, Canada from 2000 to 2004 near the towns of Newbury (42° 41′ N, 81° 48′ W), Ingersoll (43° 02′ N, 80° 53′ W), and Port Rowan (42° 35′ N, 80° 15′ W). Woodlots were a mix of privately and publicly owned properties. We selected upland hardwood forest fragments that had a minimum woodland area of 15 ha (range: 15–270 ha). Logging at the harvested sites occurred within 5 years prior to the initiation of our study (1994–99). Sites were classified into two categories based on the intensity of partial harvest. Heavy-cut sites were harvested by diameter-limit harvest and/or >33% of the initial basal area was removed ($n = 6$). The mean (±SE) basal area for heavy-cut sites was 29 ± 2 m^2/ha pre-harvest and 18 ± 1 m^2/ha post-harvest. Standard-selection sites had <33% of the basal area removed ($n = 4$), and had a mean (±SE) basal area of 27 ± 2 m^2/ha pre-harvest and 22 ± 1 m^2/ha post-harvest. Reference sites had no tree cutting for >25 years representing some of the least disturbed sites in southwestern Ontario ($n = 13$), and had a mean (±SE) basal area of 31 ± 1 m^2/ha (Table 1). Three reference stands were slightly disturbed at the time of the study, but all retained high tree densities (basal areas >28 m^2/ha); two sites had received light firewood thinning in 1980 and one had been commercially thinned under single-tree selection in 1987.

The landscape surrounding the study sites is primarily fragmented by agriculture so that woodlots are a sub-sample of a previously (ca. 1800s) more continuous Carolinian forest zone. Forest cover within a 2-km radius buffer was an average (±SD) of 31 ± 19% with 67 ± 19% agricultural cover. Dominant tree species included sugar maple (*Acer saccharum*), red maple (*A. rubrum*), white oak (*Quercus alba*), red oak (*Q. rubra*), white ash (*Fraxinus americana*), green ash (*F. pennsylvanica*), American beech (*Fagus grandifolia*), and black cherry (*Prunus serotina*) (Ontario Ministry of Natural Resources 2000).

Habitat Structure.—We sampled microhabitat at random points in eight reference sites, three standard-selection sites, and three heavy-cut sites using circular vegetation plots with a radius of 5 m. The location of 5–10

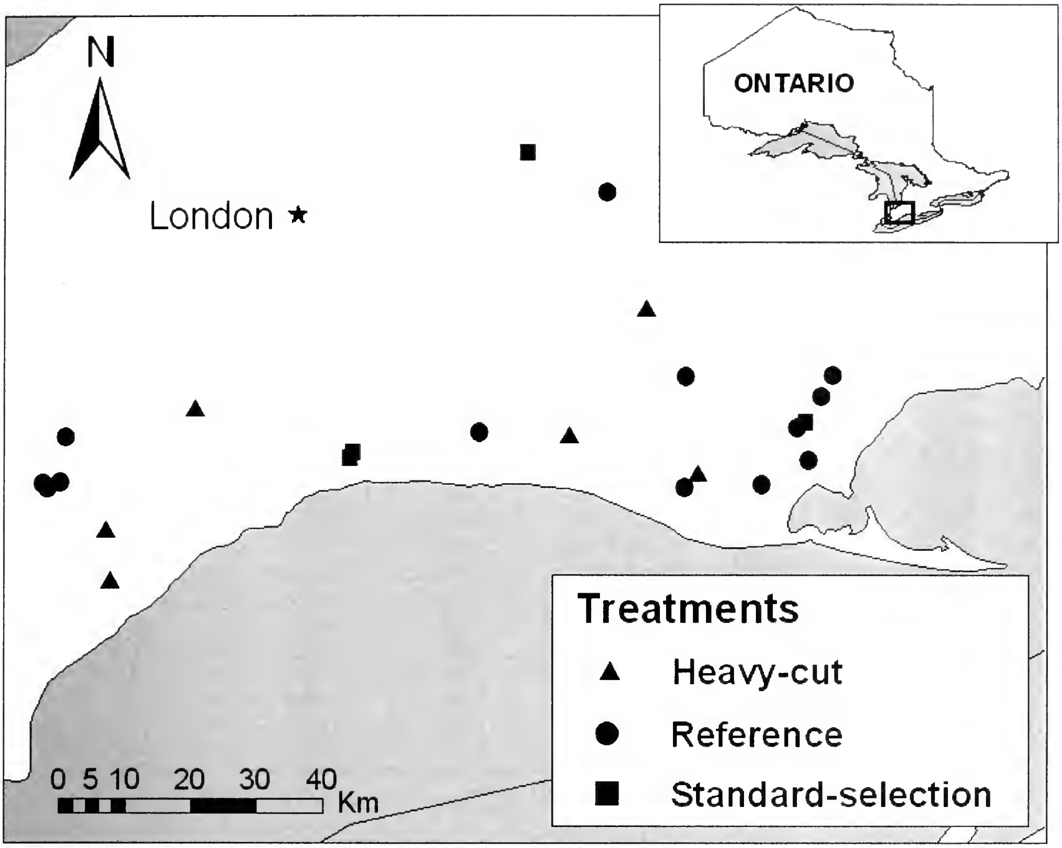

FIG. 1. Distribution of study woodlots in which Rose-breasted Grosbeak nests were monitored in southern Ontario (2000–2004) showing the interspersion of reference, standard-selection, and heavy-cut woodlots.

vegetation plots was randomly selected from a map of the study site. The closest tree able to support a grosbeak nest, (alive, diameter at breast height [dbh] >2.5 cm, tree height >1.4 m) was the center of the plot and this tree was considered to be the "random nest tree." We also sampled microhabitat at nest sites in 11 reference sites, 3 standard-selection sites and 6 heavy-cut sites also using circular vegetation plots with a radius of 5 m. Characteristics measured at nests and random sites were: center tree height and dbh, percent cover of the ground layer (soil, seedlings, forbs/grasses/ferns), regeneration cover (0.5–1.3 m high), sapling cover (>1.3 m high and <2.49 cm dbh), shrub density (density of all woody stems <2.5 cm dbh), sub-canopy cover (2.5–9.9 cm dbh), canopy cover (>10 m high), and basal area. Nest parameters included nest height, mean percent nest concealment, and mean distance to the closest tree in each of the four cardinal directions. Nest height and distance to the closest tree were measured using an electronic distance and height measuring tool (Vertex^{TM}). Percent cover was estimated visually after a standardized training session for all field assistants and basal area was calculated using a standard prism sweep (factor-2 prism). Nest concealment was estimated visually from each of the four cardinal directions (1 m from the nest), directly above and below the nest, and averaged for all six measures.

Nest Searching and Monitoring.—We searched for nests in 12 reference sites, 4 standard-selection sites, and 6 heavy-cut sites between 1 May and 31 July, 2000 to 2004, and found 214 Rose-breasted Grosbeak nests. Nest searching methods included following both males and females, especially when nest

TABLE 1. Descriptions of reference woodlots and those undergoing standard-selection and heavy-cutting in southern Ontario from 2000 to 2004. RE–Reference, SS–Standard-selection, HC–Heavy-cut, N–Nest, V–Vegetation.

Study site	Treatment	Basal area (m^2/ha)	Owner	Year of last cut	Woodland area (ha)	Samples taken[a]	No. of nests	No. of vegetation plots
501	RE	26.75	Conservation Authority[b]	<1975	161.2	N^2V	6	21
502	RE	28.42	Conservation Authority	1987	170.8	N^2V	5	21
551	RE	29.81	County Forest	1954–1966	96.9	N^3V	30	33
552	RE	30.88	County Forest	1977–1980	190.8	N^2V	8	37
401	RE	30.88	Conservation Authority	1964/1978	189.6	V	0	1
402	RE	31.18	Conservation Authority	1980	106.3	N^2V	5	4
503	RE	32.46	Conservation Authority	1976–1977	169.2	N^3V	14	38
403	RE	35.47	Conservation Authority	<1975	261.6	N^4V	11	15
553	RE	35.62	County Forest	1964	269.6	N^3V	13	37
504	RE	35.67	County Forest	<1975	181.3	N^2V	2	27
407	RE	37.16	Provincial Park	<1975	20.1	N^1V	1	1
600	RE	26.50	Conservation Authority	<1975	234.0	N^1V	5	9
451	RE	20.62	Private	1949	40.0	N^1	1	0
88	SS	19.74	Private	1994	39.7	N^1	1	0
108	SS	20.51	Private	1999	25.0	N^1V	6	24
42	SS	22.99	Private	1998	21.6	N^4V	12	28
77	SS	25.60	Conservation Authority	1995	139.9	N^2V	3	13
107	HC	14.18	Private	1997	49.6	N^3V	26	37
36	HC	15.06	Conservation Authority	1998	104.9	N^4V	16	32
86	HC	17.19	Private	1997	14.9	N^2V	4	5
300	HC	18.10	Private	1998	154.3	N^3V	10	0
121	HC	19.55	Private	1996	25.9	N^4V	19	32
111	HC	22.18	Conservation Authority	1998	53.2	N^3V	7	6

[a] Superscript number next to N represents the number of years nests were sampled.
[b] Conservation Authority refers to the Long Point Regional Conservation Authority.

building, and visual scanning of the vegetation. Efforts were made to find nests in every territory and we searched each woodlot for approximately the same number of hours, averaging 78/site to ensure equal effort. Active grosbeak nests were defined as those having eggs and/or nestlings anytime during the observation period. Parasitized nests were defined as containing a Brown-headed Cowbird (*Molothrus ater*) egg and/or nestling anytime during the observation period. We marked nests with flagging tape placed at least 5 m from nests. Nests were checked every 3–4 days, near hatch date, and then every 2 days until fledging. The number of eggs and/or nestlings, cowbird parasitism, parental activity, time of visit, and date were recorded. We assumed depredation if the nest was empty ≥2 days before the estimated fledging date. We considered a nest successful if at least one grosbeak fledged (i.e., fledglings seen near the nest, adults seen carrying food near the nest, young observed in the nest ≤2 days before expected fledging, no obvious sign of predation). Universal Transverse Mercator (UTM) coordinates were taken at nest locations using a global positioning system unit (GPS).

Statistical Analyses.—We used a nested analysis of variance (ANOVA) to compare vegetation features between nest and random sites among treatments. Terms used in the ANOVA were treatment, woodlot nested in treatment, nest or random, and the interaction effect between treatment and nest or random. Seedling cover, regeneration cover, sapling cover, and canopy cover were selected for analysis because these vegetation variables differed between treatment types at random sites (all $P < 0.05$) (Smith et al. 2006). A nested ANOVA was used to examine if nest height and nest concealment varied between treatments, and the Tukey test for unequal sample sizes was used to examine *post-hoc* significance. Independent *t*-tests were performed to examine whether parasitized and non-parasitized nests could be distinguished by the same five vegetation characteristics that varied among treatments. We tested for normality using the Kolmogorov-Smirnov one-sample *D*-statistic and transformed data accordingly. We did not use the sequential Bonferroni technique because it is considered to be overly conservative and increases the chance of a Type II error (Nakagawa 2004). All results are reported as mean ± SE.

Modeling.—The logistic-exposure method (Shaffer 2004) was used to estimate daily nest-survival rates for Rose-breasted Grosbeaks. Model selection was based on the information-theoretic approach which allows the researcher to build models and examine support for alternative models based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Our model was based on a binomial distribution (interval nest fate = 1 if successful and 0 if failed) to identify and evaluate factors responsible for changes in nest survival (Shaffer 2004). The time between nest checks was often >1 day, and we used the modified logit link function: $g(\theta) = \log_e(\theta^{1/t}[1 - \theta^{1/t}])$, where t is the interval length in days and θ is the interval survival rate (Shaffer 2004). *A priori* models were fitted with PROC GENMOD (SAS Institute 2001) by selecting a binomial response distribution and the modified logit link function.

We hypothesized that silvicultural practices alter the vegetative structure of the woodlot, and in turn, these vegetation features affect nest survival and based model selection on the careful definition of candidate models (Burnham and Anderson 2002). Individual features (e.g., canopy cover) may predominate or vegetation characteristics could be acting together; therefore, we included several additive vegetation models. We addressed possible sources of variation in survival through a series of *a priori* hypotheses. (1) Canopy cover: a vegetation characteristic that is widely affected by forestry practices and alters the original stand structure through the removal of canopy and sub-canopy trees. A decrease in canopy cover has been associated with changes in nest success for other species (positively for Yellow-breasted Chats [*Icteria virens*; Ricketts and Ritchison 2000], and negatively for Wild Turkeys [*Meleagris gallopavo*; Nguyen et al. 2004] and Acadian Flycatchers [*Empidonax virescens*; Wilson and Cooper 1998]). We hypothesized that canopy cover should predict daily survival rates for Rose-breasted Grosbeaks since this vegetative feature is selected for nest sites (Smith et al. 2006). (2) Concealment: nest concealment is a logical factor to include when examining the effects of vegetation on daily survival rates, although current literature is conflicting and few studies have actually found concealment to be associated with nest success. Howlett and Stutchbury (1996) and Peak (2003) showed that concealment was not associated with predation rates for Hooded Warblers (*Wilsonia citrina*) and American Goldfinches (*Carduelis tristis*), respectively. Alternatively, Liebezeit and George (2002) and Martin and Roper (1988) both demonstrated a decrease in predation rates with an increase in nest concealment for Dusky Flycatchers (*Empidonax oberholseri*) and Hermit Thrushes (*Catharus guttatus*), respectively. (3) Nest height: daily survival rates should be highest at nests which are placed higher as this may make nests less accessible to ground predators (Murphy 1983, Wilson and Cooper 1998). (4) Sapling cover: cover in the sapling layer (>1.3 m high and <2.5 cm dbh) was another vegetation feature that Rose-breasted Grosbeak's selected when choosing a nest-site (Smith et al. 2006). Therefore, sapling cover should be important in predicting daily survival rates and has been shown to be important for other species in predicting nest success (Dusky Flycatchers; Liebezeit and George 2002). (5) Distance to the edge of the woodlot (>100 m or ≤100 m): we also hypothesized that proximity to the edge of the habitat might influence nest survival by influencing nest predation rates (Woodward et al. 2001, Albrecht 2004, Batary and Baldi 2004). Candidate models included nest height, sapling cover, canopy cover, average nest concealment, distance to the edge of the woodlot, a variety of additive models based on these parameters, and a null model with only an intercept. We evaluated a set of 30 models using AIC_c.

Comparing model support allowed us to identify which model was most parsimonious and most closely reflected the actual data. We calculated Δi to examine the difference between the AIC_c for each candidate model and the model with the lowest AIC_c score. Akaike weights (w_i) were calculated for each model

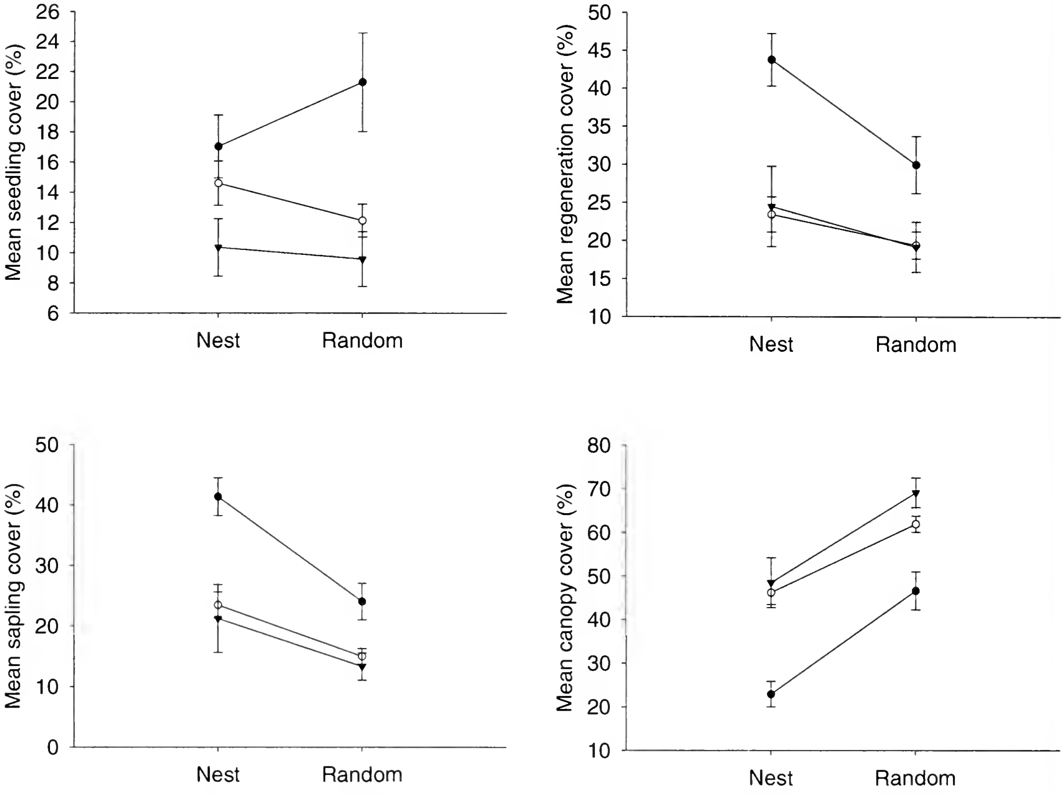

FIG. 2. The effect of forestry treatment type on Rose-breasted Grosbeak nest-site selection in southern Ontario (2000–2004). Closed circles represent heavy-cut sites, open circles represent reference sites, and triangles represent standard-selection sites. Sample sizes are n = 90 nests and n = 154 random plots in reference sites, n = 23 nests and n = 51 random plots in standard-selection sites, and n = 77 nests and n = 45 random plots in heavy-cut sites. Means with standard errors are shown.

to examine the relative likelihood of the model given the data. These resulting weights sum to one across all models and are interpreted as probabilities where a model with an Akaike weight approaching one is strongly supported by the data (Johnson and Omland 2004). We present the model averaged parameter estimates, standard errors, and 95% confidence intervals due to high model selection uncertainty (models with $\Delta AIC_c < 7$ compared to the top model).

RESULTS

Nest-site selection was not influenced by the amount of seedling cover, as Rose-breasted Grosbeaks selected nest sites with percent seedling cover (15 ± 1.1%) similar to that at random sites (13 ± 1.0%; $F_{1,415} = 0.35$, $P = 0.56$; Fig. 2). There was also no difference in the amount of regeneration cover between nest sites (32 ± 2.0%) and random sites (21 ± 1.5%; $F_{1,415} = 3.35$, $P = 0.068$; Fig. 2). However, there was a tendency for percent cover of the regeneration layer to be higher at nest sites. There was a significant interaction effect for sapling cover between the nest or random term and treatment term ($F_{2,415} = 6.43$, $P = 0.002$); therefore, we looked at sapling cover among treatments only for nests. Rose-breasted Grosbeaks selected nest sites with significantly more sapling cover in heavy-cut sites (41 ± 3.1%) than in standard-selection (21 ± 5.6%) and reference sites (24 ± 2.2%; $F_{2,19} = 6.77$, $P = 0.002$; Fig. 2). Canopy cover was significantly lower in all treatments at nest (37 ± 2.1%) than at random sites (61 ± 1.6%; $F_{1,415} = 57.91$, $P < 0.001$; Fig. 2). Nest sites also had significantly lower basal area (18 ± 0.6%) than random sites (23 ± 0.5%; $F_{1,414} = 7.64$, $P = 0.006$; Fig. 2)

TABLE 2. Nest-site microhabitat at parasitized and non-parasitized Rose-breasted Grosbeak nests in southern Ontario (2000–2004). Values were measured across all treatment types.

	Non-parasitized		Parasitized				
Vegetation variable	Mean ± SE	n	Mean ± SE	n	t	df	P
Diameter at breast height, dbh	6.8 ± 0.83	91	6.9 ± 3.99	10	1.51	99	0.14
Nest height, m	4.3 ± 0.35	91	2.9 ± 0.65	10	2.33	99	0.022[a]
Regeneration, %	34.9 ± 3.11	91	57.9 ± 9.14	10	1.99	99	0.050[a]
Sapling cover, %	36.3 ± 2.72	91	31.8 ± 8.14	10	0.52	99	0.60
Sub-canopy cover, %	33.0 ± 2.41	91	21.6 ± 8.18	10	1.47	99	0.14
Canopy cover, %	30.7 ± 2.87	91	27.2 ± 6.43	10	0.40	99	0.69
Mean nest concealment, %	65.5 ± 2.27	91	63.2 ± 8.37	10	0.32	99	0.75
Mean distance of closest tree, m	7.4 ± 0.30	91	7.9 ± 1.11	10	0.45	99	0.65

[a] Significant P value.

across all treatments. Rose-breasted Grosbeak nests were placed significantly lower in heavy-cut sites (4.38 ± 0.49 m) than in both standard-selection (11.0 ± 1.8 m) and reference sites (8.46 ± 0.76 m; $F_{2,19} = 8.27$, $P = 0.001$). Rose-breasted Grosbeak nests were more concealed in heavy-cut sites (74 ± 2.4%) and standard-selection sites (73 ± 4.1%) than reference sites (65 ± 3.0%; $F_{2,19} = 1.36$, $P = 0.26$), although the difference in concealment between heavy cut and reference sites was only approaching significance (*post-hoc* $P = 0.055$).

One hundred and ninety-three of 214 nests monitored had sufficient observations (more than one visit while the nest was still active) to be included in the nest-survival analysis; this resulted in 405 observation intervals (based on the time between nest checks). The daily survival rate (DSR) over 1,725 observation days was 0.9612 and nest success was 0.39, indicating that only 39% of nests survived the 22 days from incubation to fledging. One hundred and fifty-one of the 214 nests monitored had known outcomes with respect to predation events. Predation rate was high as 95 of 151 nests were depredated (63%). Only 16 (12%) of 138 nests for which contents were known were parasitized by Brown-headed Cowbirds. Nests that were parasitized were significantly lower in height and had significantly more regeneration cover at the nest-site than nests that were not parasitized (Table 2).

The best supported model explaining variation in daily nest survival was based on that which included nest concealment alone with the lowest AIC_c and the highest Akaike weight (Table 3). Models including distance-to-edge, canopy cover, sapling cover, and nest height were not highly supported and only gained moderate support when included in any model containing nest concealment. All models containing the nest concealment parameter ranked in the top 15 models with weights ranging from 0.287 to 0.007. Additional variables did not increase the parsimony of the model. Concealment produced a model-averaged estimate with a negative slope indicating higher nest survival when nests are less concealed (Table 4). Model-averaged estimates produced positive slopes for canopy cover, sapling cover, and nest height indicating higher survival at higher measures of these parameters. Model-averaged estimates of distance-to-edge showed a negative response, indicating a higher probability of survival within 100 m from the edge of the woodlot.

DISCUSSION

Rose-breasted Grosbeaks showed plasticity in nest-site selection by choosing nest-site parameters that differed across treatments. In woodlots with varying amounts of tree removal and in reference stands, nests were most often placed in areas with less canopy cover, more sapling cover, lower basal area, and a tendency for more regeneration cover than at random locations within those sites. However, the absolute value of these parameters often differed between treatments.

Woodlots subjected to heavy, diameter-limit harvests had a vegetative structure that favored nest-site selection preferences of the Rose-breasted Grosbeak. Sites with higher in-

TABLE 3. Model support for hypotheses that sapling cover, canopy cover, nest concealment, nest height, and distance-to-edge influence the daily survival rates (DSR) of Rose-breasted Grosbeak nests (2000–2004, southern Ontario). Log-likelihood values, the number of model parameters (K), Akaike's Information Criterion corrected for small sample size (AIC_c), Δi (AIC_c model i − AIC_c minimum), and Akaike weights (w_i) are shown for 30 logistic-exposure models.

Model	Log-likelihood	K	AIC_c	Δi	w_i
$\text{DSR}_{\text{concealment}}$	−161.28	2	326.57	0.000	0.287
$\text{DSR}_{\text{concealment + distance-to-edge}}$	−161.22	3	328.46	1.887	0.112
$\text{DSR}_{\text{concealment + canopy}}$	−161.22	3	328.46	1.889	0.111
$\text{DSR}_{\text{concealment + sapling}}$	−161.22	3	328.46	1.891	0.111
$\text{DSR}_{\text{concealment + nest height}}$	−161.26	3	328.54	1.972	0.107
$\text{DSR}_{\text{concealment + sapling + canopy}}$	−161.08	4	330.19	3.626	0.047
$\text{DSR}_{\text{concealment + sapling + distance-to-edge}}$	−161.16	4	330.34	3.773	0.044
$\text{DSR}_{\text{concealment + sapling + distance-to-edge + nest height}}$	−161.17	4	330.37	3.800	0.043
$\text{DSR}_{\text{concealment + nest height + distance-to-edge}}$	−161.20	4	330.42	3.855	0.042
$\text{DSR}_{\text{concealment + nest height + canopy}}$	−161.22	4	330.47	3.900	0.041
$\text{DSR}_{\text{concealment + canopy + nest height + sapling}}$	−161.08	5	332.20	5.628	0.017
$\text{DSR}_{\text{concealment + nest height + sapling + distance-to-edge}}$	−161.10	5	332.24	5.673	0.017
$\text{DSR}_{\text{concealment + canopy + nest height + distance-to-edge}}$	−161.18	5	332.39	5.823	0.016
$\text{DSR}_{\text{concealment + canopy + nest height + distance-to-edge + sapling}}$	−161.04	6	334.13	7.560	0.007
$\text{DSR}_{\text{constant}}$	−170.25	1	342.50	15.932	<0.001
$\text{DSR}_{\text{canopy}}$	−169.84	2	343.68	17.110	<0.001
$\text{DSR}_{\text{nest height}}$	−170.10	2	344.22	17.646	<0.001
$\text{DSR}_{\text{distance-to-edge}}$	−170.17	2	344.34	17.773	<0.001
$\text{DSR}_{\text{sapling}}$	−170.25	2	344.50	17.929	<0.001
$\text{DSR}_{\text{canopy + sapling}}$	−169.78	3	345.57	19.005	<0.001
$\text{DSR}_{\text{canopy + distance-to-edge}}$	−169.79	3	345.61	19.037	<0.001
$\text{DSR}_{\text{canopy + nest height}}$	−169.83	3	345.68	19.114	<0.001
$\text{DSR}_{\text{distance to edge + nest height}}$	−170.01	3	346.03	19.462	<0.001
$\text{DSR}_{\text{nest height + sapling}}$	−170.10	3	346.21	19.646	<0.001
$\text{DSR}_{\text{distance-to-edge + sapling}}$	−170.16	3	346.34	19.775	<0.001
$\text{DSR}_{\text{distance-to-edge + canopy + sapling}}$	−169.74	4	347.51	20.940	<0.001
$\text{DSR}_{\text{sapling + nest height + canopy}}$	−169.77	4	347.57	21.003	<0.001
$\text{DSR}_{\text{distance-to-edge + canopy + nest height}}$	−169.79	4	347.60	21.036	<0.001
$\text{DSR}_{\text{distance-to-edge + nest height + sapling}}$	−170.00	4	348.03	21.460	<0.001
$\text{DSR}_{\text{distance-to-edge + sapling + nest height + canopy}}$	−169.73	5	349.50	22.931	<0.001

tensity harvests had denser regeneration and sapling layers, and more open canopy than sites with less intensive wood removal (Smith et al. 2006). Rose-breasted Grosbeaks nested lower and tended to have more concealed nests in heavy-cut sites. Although these features were selected for nesting, lower canopy cover, lower nest heights, and increased concealment in particular, appear to be maladaptive, and confer lower nest success. In heavy-

TABLE 4. Model-averaged estimates, standard errors, and 95% confidence intervals based on 30 nest survival models (n) for Rose-breasted Grosbeak nests (2000–2004, southern Ontario).

Parameter	Model-averaged parameter estimate	n	Standard error	95% Confidence interval
Intercept	3.354	30	0.589	2.196–4.512
Canopy cover	0.040	30	0.139	−0.233–0.313
Concealment	−0.344	30	0.520	−1.367–0.678
Sapling cover	0.053	30	0.169	−0.279–0.385
Distance-to-edge (far = 1, near = 0)	0.020	30	0.075	−0.127–0.167
Nest height	0.022	30	0.137	−0.247–0.291

cut sites, the pervasiveness of a more open canopy would present an ecological trap and reduce nest success for this species across these sites (Gates and Gysel 1978). As much as 94% of the cuttings in some regions of southern Ontario are heavy-cuts (T. D. Schwan, unpubl. data) and much of eastern North America hardwood forests are harvested this way (Nyland 1992). Thus, these ecological traps could help explain the significant annual declines in the abundance of this species as measured by Breeding Bird Survey data (Sauer et al. 2004). Presumably as the forest matures, the vegetation will change and become more similar to reference conditions. These conditions should lead to higher nest success, but they may be selected less frequently because of this species' seeming "innate" preference for lower canopy cover. This might explain why Rose-breasted Grosbeaks occur at high densities in heavily harvested woodlots in southern Ontario (Smith et al. 2006), despite lower nest survival rates.

Nest-site vegetation also influenced the probability that a nest would be parasitized. Nests in locations with higher cover of woody regeneration and at lower nest heights were significantly more likely to be parasitized. This is similar to results found elsewhere on the importance of nest height for Acadian Flycatchers, with non-parasitized nests placed typically higher than parasitized nests (Wilson and Cooper 1998). Brown-headed Cowbirds largely focus on adult behavior in finding nests to parasitize (Lowther 1993). It may be easier for female cowbirds to follow adults through the understory when perched in the canopy than for them to find nests in the canopy (Wilson and Cooper 1998). In our study, regeneration cover was significantly higher in heavy-cut sites and grosbeaks nested lower in these sites. This could pose an additional threat to nest success or host productivity. However, Rose-breasted Grosbeaks are not a preferred host (Wyatt and Francis 2002). The uncommon bi-parental incubation pattern exhibited by Rose-breasted Grosbeaks results in the nest being unattended for less time (Wyatt and Francis 2002) and may reduce parasitism events on this species. Parasitism rates are low for this species and parasitism is probably not driving the extensive declines in Rose-breasted Grosbeak populations in southern Ontario. Parasitism contributed little to nest survival estimates and productivity for grosbeaks, but for many species where parasitism rates are high, it may be an important conservation issue. Heavy-cut sites in our region have greater densities of Brown-headed Cowbirds in general (Holmes et al. 2004) and harvest-related changes in the vegetation structure that favor cowbirds may put some populations at greater risk.

Our results suggest that partial harvesting practices create potential nest sites for Rose-breasted Grosbeaks by providing "preferred" vegetation characteristics. These logging regimes, particularly heavy-cutting, simultaneously create stands that are characterized by habitat features that proliferate high parasitism rates and lower daily survival rates than are typical of reference stands. Rose-breasted Grosbeaks consistently selected nest sites with a reduced basal area, a tendency for more regeneration, more sapling cover, less canopy cover, and this preference became stronger in woodlots that had been harvested to a low residual basal area (heavy-cut sites). However, daily nest survival rates were lower when grosbeaks selected lower nests, nests in areas of lower canopy, and higher nest concealment as in heavy cut sites, which are preferred nest-site characteristics. This demonstrates an inability to select features that confer high success, despite theory (Martin 1998). We found nest-site selection was based on proximate vegetation cues which varied relative to the silvicultural prescription, and ultimately had negative reproductive consequences for the Rose-breasted Grosbeak.

There are limits to this study as we were unable to assess directly the impacts of logging, because we do not have measurements of nest-site selection and survival on study sites prior to logging. However, the loss of canopy cover that occurs as a direct result of logging should create nest-site habitat for this species, yet simultaneously reduce overall productivity of birds nesting on those sites. Heavy logging at a landscape scale may contribute towards population declines in Rose-breasted Grosbeaks by providing a large amount of preferred nesting habitat that ultimately confers poor nesting success. Further studies should involve experimental research to monitor how grosbeaks respond directly to changes in habitat post-logging to document the intensity and nature of these relationships, and the possibility of logging creating ecological traps.

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REPRODUCTIVE SUCCESS AND NEST DEPREDATION OF THE FLORIDA SCRUB-JAY

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ABSTRACT.—The Florida Scrub-jay (*Aphelocoma coerulescens*) is listed as a threatened species primarily because of habitat loss throughout much of its range. The Ocala National Forest in Florida contains one of three main subpopulations that must be stable or increasing before the species can be considered for removal from federal listing. However, little information is available on Florida Scrub-jay reproductive success or predation pressure on this forest. I used video cameras during 2002 and 2003 to identify nest predators and timing of predation events. The presence of the video system did not significantly affect the rate of nest abandonment. Thirteen nests were video-monitored of which one was abandoned, five experienced no predation, three were partially depredated, and four had total loss of nest contents. Snakes were responsible for more losses from predation than either mammals or birds. I monitored 195 other scrub-jay nests (no video-monitoring) and measured the mean number of eggs, nestlings, and fledglings produced per breeding pair. No significant difference in reproductive success was detected between years or between year and helper status. Groups with helpers produced significantly more fledglings (0.5 per breeding pair) and had higher daily survival rates of nests in the egg stage, nestling stage, and the entire breeding season than groups lacking helpers. *Received 15 July 2005. Accepted 7 October 2006.*

The Florida Scrub-jay (*Aphelocoma coerulescens*), federally listed as a threatened species, occurs primarily on lands containing fine, well-drained soils along Florida's coastline, and on ancient sand dune ridges in the interior of peninsular Florida. They are monogamous cooperative breeders living in groups on year-round territories. Groups contain a mated pair and as many as six helpers that may be related to one or both members of the breeding pair (Sprunt 1946, Woolfenden 1978). Helpers do not build nests, incubate, feed the incubating female, or brood, but do feed nestlings and fledglings, and also participate in mobbing possible predators (Woolfenden and Fitzpatrick 1984). Pairs will renest if the nest is lost in an effort to produce one brood of fledglings per breeding season (Woolfenden and Fitzpatrick 1984). Preferred habitat consists of dense thickets of scrub oaks (*Quercus* spp.) <3 m tall with bare sand substrate between them and may develop after land has been burned, harvested, or otherwise cleared. The amount of new habitat currently is inadequate and, coupled with conversion of existing habitat for silviculture, agriculture, commercial as well as residential development, has led to an overall reduction in the amount of suitable scrub-jay habitat (Fitzpatrick et al. 1991).

The Ocala National Forest in Florida has a crucial role in the recovery of this species. Three meta populations, Ocala National Forest, Merritt Island/Cape Canaveral, and Lake Wales Ridge (Archbold Biological Station near Lake Placid, Florida), must be stable or increasing before the species can be considered for delisting by the U.S. Fish and Wildlife Service (U.S. Department of Interior [USDI] 1990). The Florida Scrub-jay is limited geographically because of its specific habitat requirements. The population on the Ocala National Forest was estimated to be 2,600–3,400 birds in the 1980s (Cox 1987); current estimates are 851 groups with 2,341 birds (L. S. Lowery, pers. comm.). Information is needed for the Ocala National Forest population on optimal habitat conditions, survival of young and adults, nesting, reproductive success, dispersal, mortality, predation, and territory configuration. A preliminary study in 2001 indicated nest loss was high and mean (± SE) reproductive success was only 2.25 ± 0.31 fledglings/successful nest (n = 8) or 0.60 ± 0.20 fledglings/nesting pair (n = 30; KEF, unpubl. data). Woolfenden and Fitzpatrick (1984) suggested that most nest losses are the result of nest predation. The objectives of my study were to: (1) examine whether pre-

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dation pressure was affecting nesting success; (2) identify whether year or the presence of helpers affected reproduction in the egg stage, nestling stage, or in the number of fledglings produced per breeding pair; and (3) evaluate nest success (daily survival rate of nests) in different stages of the nesting cycle comparing 2002 to 2003 and nests with helpers to those without helpers.

METHODS

Study Area and Banding.—The study was conducted on the Ocala National Forest between Gainesville and Daytona Beach, Florida in Marion, Lake, and Putnam counties. Scrub-jays were trapped using a modified Potter trap and banded with federal aluminum bands and a unique combination of plastic colored leg bands to facilitate field identification. Approximately 69% of video-monitored nests and 30% of observer-monitored nests had pairs in which at least one member was banded. All nestlings in monitored nests were banded if they survived to 10 days of age.

Data Collection.—Nests were selected by randomly driving or walking slowly along sandy, one-lane tracks that are numerous in the area until a group of jays was detected and then observing the birds to locate the nest. Thus, most nests were relatively close to one-track roads, which provided efficient access to territories and nests. There was little human foot traffic to disturb nesting birds or to influence predator movement patterns. Camera equipment was placed under concealing vegetation to minimize the likelihood that equipment would be observed, disturbed, or stolen.

Nests were monitored using two Fieldcam LDTLV video recording systems that consisted of a Sony SVT-LCc300 time lapse videocassette recorder (VCR) in a weatherproof case and a MicroCam 2 black-and-white infrared camera equipped with infrared emitters for night recording (Fuhrman Diversified, Inc., Seabrook, TX, USA) (use of brand names does not convey a recommendation of the product by the U.S. Forest Service). Cameras were mounted on an articulated arm for nests monitored in 2002. A 20-m cable connected the camera to the VCR, which was powered by one or two 12-volt deep-cycle batteries (two batteries if the recording session was going to last longer than 48 hrs). The camera was attached immediately adjacent to the nest shrub and positioned so it was on average 46 cm from the nest. Camera height varied from being level with the nest to as high as 46 cm above it depending on how the branches were arranged close to the nest. The cable connecting the camera to the VCR was placed on top of small shrubs to prevent damage by rodents. I attached the camera directly to a branch above the nest on the shrub in 2003. Placing the camera equipment at a nest required between 5 and 15 min. I replaced video cassettes (T-160) and batteries every 48–72 hrs. Battery replacement required about 5 min. There were no obvious displays of distress by the birds during that time. The lack of agitation was attributed to the VCR being 15–20 m from the nests so the observer did not have to visit the nest itself other than to install the camera on the initial visit. The VCR recorded images at a rate of one every 0.083 and 0.150 sec when operating in 48- and 72-hr modes, respectively.

I monitored 13 Florida Scrub-jay nests (6 in 2002 and 7 in 2003) between 2 May and 7 July 2002, and 9 April and 5 May 2003. One of these nests, monitored during the egg stage from 10 to 11 May 2002, was abandoned the day after the camera was installed. This nest was not included in the predation analysis. Considering the 13 nests, seven had both members of the pair banded, two had one member banded, and four had neither pair member banded. No pairs were monitored in both 2002 and 2003.

The video camera systems were installed either during incubation (n = 11) or after the eggs had hatched (n = 2). Three types of depredation events were characterized in this study: a total depredation event in which all nest contents were taken at the same time; a partial depredation event in which a predator took only part of the nest contents; and a sequential-complete depredation event when one or more predators visited the same nest multiple times until all the nest contents had been removed.

An observer periodically visited the 195 other nests (73 in 2002 and 122 in 2003) that were not video equipped approximately every 3 days, more frequently around the expected date of hatching or fledging. The observer recorded the number of eggs present, number of eggs hatched, number of nestlings, and number of fledglings. These same variables were obtained for video-monitored nests by analyzing content of the video tapes. It is possible that in some cases one or more eggs were removed from the nest before the nest was first observed. Brown-headed Cowbird (*Molothrus ater*) nest parasitism does not appear to be a problem for this species. The number of fledglings was ascertained by frequent visits to the nest around the anticipated time of fledging. Nests that failed to fledge young were distinguished from successful nests by looking for indications the nest had been disturbed or damaged, and by looking for direct evidence of depredation such as loose feathers. Evidence of fledging included feces on the edge of the nest or on the ground beneath it. Occasionally a fledgling was observed in the nest site area immediately after the suspected fledging event, but more often they were seen at a later date and identified because they were banded.

Daily Survival Rates and Exposure Days.—I used the Mayfield method (Mayfield 1961, 1975) to assess nest success. The number of days that each nest is observed and is subject to failing is referred to as exposure days. Dividing the number of nests known to have failed by the sum of the total exposure days results in the daily mortality rate (DMR) or probability the nest will fail on any day. The daily survival rate (DSR), defined as the probability of the nest contents (at least one egg or nestling) surviving from one day to the next, is estimated as $1 - \text{DMR}$. I calculated the daily survival rate of the nest for the egg stage, nestling stage, and for the entire breeding season for each year and for both years combined for all nests, and then for nests with helpers and those without helpers following Mayfield (1961, 1975). The Mayfield method was calculated on a per nesting attempt basis and not on a per breeding pair basis. I defined egg stage to include laying and incubation. I deleted those nests for which the helper status was unclear or unknown for the Mayfield calculations.

Statistical Analysis.—Data from nests were segregated by year (2002, 2003), type of monitoring (video, observer), and group helper status (no helper, one or more helpers, or helper status unknown). Groups in which helper status could not be verified were excluded from all results except in assessment of nest abandonment. I used the log-likelihood ratio (*G*-test; Sokal and Rohlf 1995) to compare rate of nest abandonment for nests with video cameras to those that were observer-monitored. Means ± SE are reported.

It may be improper to pool data for analysis of reproductive success if a nest found in the egg stage has a different likelihood of producing fledglings than one found in the nestling stage. I segregated data for observer-monitored nests by whether the nest was found in the egg or the nestling stage, and further by year and group helper status (groups with no helpers vs. groups with at least one helper). I used *G*-tests to compare the reproductive success of pairs, whose nests were found in the egg stage, belonging to groups with and without helpers for each year. I performed the same test for the nestling stage. I combined the data for groups with and without helpers and evaluated it using a *G*-test to assess whether time of the nesting cycle (egg vs. nestling) in which the nest was found influenced reproductive success.

I used two-way analysis of variance (ANOVA; Sokal and Rohlf 1995) using PROC GLM (SAS Institute 1989) to examine the possible effect of year and helper status on the number of eggs, nestlings, and fledglings produced per breeding pair. Only observer-monitored nests were included in this part of the analysis. ANOVA was used to detect possible interactions between year and helper status on reproductive success. Least-squares means were used to examine the mean number of eggs, nestlings, and fledglings produced per breeding pair for data segregated by year and helper status (SAS Institute 1989).

I combined data for 2002 and 2003 and examined data separately for pairs with helpers and those that lacked helpers to examine losses from the egg to nestling and from the nestling to fledgling stages. Only nests found during the egg laying or incubation stage and for which helper status was confirmed were included in this part of the analysis. The total numbers of eggs, nestlings, or fledglings for groups with helpers were compared to groups without helpers with a *G*-test. All *G*-tests and ANOVA tests were performed at the 0.10 significance level to reduce the type II error.

TABLE 1. Abandonment per nesting attempt of video- versus observer-monitored Florida Scrub-jay nests on the Ocala National Forest, 2002–2003[a].

	Video (*n*)	Observer (*n*)	Totals
Not abandoned	11	184	195
Abandoned	2[b]	11	13
Totals	13	195	208

[a] Includes nests for which helper status was undetermined.

[b] Includes one nest abandoned after 28 days of incubation (video-monitored for 25 days).

I calculated standard errors for daily nest survival rates following Nur et al. (1999). Daily survival rates of nests were compared for: (1) the egg versus the nestling stage for each year and then for both years combined, (2) the egg and nestling stages for 2002 versus 2003, and (3) pairs with and without helpers using the Chi-square test in program CONTRAST (Hines and Sauer 1989).

RESULTS

Incidence of Nest Abandonment.—There were 208 nesting attempts (defined as a pair laying at least one egg) in 2002 and 2003 of which 13 were monitored by video cameras, including one nest that was abandoned shortly after the video camera was installed (Table 1). One-hundred ninety-five nests were observer-monitored of which 11 (6%) were abandoned compared to two (15%) of 13 nests that were video-monitored. One of these two nests contained infertile eggs that were eventually abandoned after 28 days of incubation (including 25 days of video monitoring). The overall rate of nest abandonment did not differ between observer- and video-monitored nests ($G = 1.52$, df $= 1$, $P = 0.234$).

Nest Predation.—All nests video-monitored were in either myrtle oak (*Quercus myrtifolia*) or sand live oak (*Q. geminata*) and 10 of 12 were at least 100 cm from the ground. These results exclude the one nest that was abandoned immediately after the camera was installed. The number of exposure days for nests varied from 6 to 37. Eight fledglings were produced in 2002; two of the five nests experienced no predation and produced seven fledglings. One nest experienced partial predation by an eastern coachwhip snake (*Masticophis flagellum*); the snake ate one of two nestlings (one disappeared before the camera was installed), and the remaining nestling eventually fledged. All contents of two other nests, consisting of two nestlings each, were lost to predation from a spotted skunk (*Spilogale putorius*) and a gray fox (*Urocyon cinereoargenteus*). Two of six nests in 2003 experienced no predation, producing six fledglings. One nest was partially depredated (one nestling taken, one fledgling produced) by an eastern coachwhip snake and another nest with one egg and two nestlings was depredated by a presumed corn snake (*Elaphe guttata*). One nest was visited on four occasions by a snake, most probably a corn snake, and one nestling was removed on each visit. An American Crow (*Corvus brachyrhynchos*) was the only avian predator and consumed all three eggs in one nest. All partial nest predation was the result of snakes, whereas predation by birds or mammals resulted in loss of the entire contents of the nest. One nest in 2003, consisting of two infertile eggs, was abandoned after being incubated for 28 days.

Twelve nests were video-monitored and 4 eggs and 13 nestlings were taken by predators while 15 fledglings were produced. Thirteen of these 15 fledglings were from five nests that experienced no predation. An additional four nests lost one egg and nine nestlings to snakes and produced two fledglings. Three eggs and four nestlings in three nests were lost to mammalian or avian predators. Four of five nests with helpers were depredated versus two of seven nests without helpers. Seven of the 10 instances of predation were nocturnal events.

Reproductive Success for Nests in the Egg Versus the Nestling Stage.—Approximately 14% (15 of 108 nests) of nests without and 25% (12 of 48 nests) of the nests with helpers were located in the nestling, rather than the egg stage. I detected no difference in 2002 in the proportion of nests that produced fledglings in groups without versus those with helpers for nests first found during the egg ($G = 0.54$, df $= 1$, $P = 0.476$, $n = 39$) or nestling stage ($G = 0.77$, df $= 1$, $P = 0.409$, $n = 17$). I combined the 2002 data for groups with and without helpers and detected no difference in the proportion of nests producing fledglings between nests found in the egg versus those in the nestling stage ($G = 0.02$, df $= 1$, $P = 0.893$, $n = 56$).

I detected no difference in the proportion of nests in 2003 first found in the egg stage producing fledglings for groups with compared to those without helpers ($G = 0.99$, df = 1, $P = 0.345$, $n = 37$). There were no differences detected for nests first found in the nestling stage for groups with and without helpers ($G = 0.75$, df = 1, $P = 0.415$, $n = 11$). I combined the data in 2003 for nests with and without helpers and the proportion of nests producing fledglings was similar regardless of whether the nest was first located in the egg or nestling stage ($G = 1.28$, df = 1, $P = 0.262$, $n = 48$). Thus, there was no sampling bias for fledging success between nests first encountered during the egg stage versus those first found in the nestling stage.

Reproductive Success per Breeding Pair in Observer-monitored Nests.—The least-squares means for reproductive success per breeding pair for observer-monitored nests were similar in 2002 and 2003 for eggs (3.29 ± 0.28 vs. 3.29 ± 0.20), nestlings (2.50 ± 0.24 vs. 2.37 ± 0.19), and fledglings (2.16 ± 0.25 vs. 1.79 ± 0.19; all P-values ≥ 0.248). I detected no difference in least-squares means in the number of eggs (3.17 ± 0.29) in nests of groups with helpers compared to nests lacking helpers (3.41 ± 0.17; $F_{1,99} = 0.50$, $P = 0.480$). I did not detect a difference in the number of nestlings produced in nests with (2.56 ± 0.26) versus those without helpers (2.30 ± 0.16; $F_{1,109} = 0.75$, $P = 0.390$). However, the number of fledglings produced per breeding pair was higher for groups with (2.24 ± 0.27) versus groups without helpers (1.71 ± 0.17) ($F_{1,109} = 2.90$, $P = 0.091$). I detected no significant interaction effects between year and helper status in observer-monitored nests in the number of eggs, nestlings, or fledglings produced per pair (all P-values ≥ 0.390).

Fifty-nine percent of the 263 eggs in nests without helpers survived to become 155 nestlings and 79% of nestlings eventually became 123 fledglings. In groups with helpers, 86 of 111 eggs (77%) survived to the nestling stage, of which 70 (81%) fledged. Combining the data for non-helper and helper groups, 241 (64.4%) of 374 eggs succeeded in becoming nestlings, of which 193 (80%) became fledglings.

Daily Survival Rates and Exposure Days.—There were 203 exposure days (12 video-monitored nests) of which 95 were egg days and 108 were nestling days. There were 2,906 exposure days for the 177 observer-monitored nesting attempts in 2002 and 2003, including 1,497 days in the egg stage and 1,409 in the nestling stage.

Nests with helpers during the egg stage in both 2002 and 2003 had a similar daily survival rate to nests without helpers ($P = 0.181$ and $P = 0.139$, respectively; Table 2). For observer-monitored nests, in both 2002 and 2003, I detected no difference between daily survival rates in the egg stage versus the nestling stage for all nesting attempts, for nests of groups with helpers, or for nests of groups without helpers (all P-values >0.370; Table 2).

The daily survival rate for nests in 2002 with helpers in the nestling stage (DSR = 0.980 ± 0.012) was higher than for nests without helpers (DSR = 0.954 ± 0.009; $\chi^2 = 3.00$, df = 1, $P = 0.083$; Table 2). I detected a higher daily nest survival rate for nests in 2003 in the nestling stage of groups with helpers than those without helpers (DSR = 0.956 ± 0.012 and 0.924 ± 0.012, respectively; $\chi^2 = 3.56$, df = 1, $P = 0.059$; Table 2).

The daily nest survival rates for 2002 combined with 2003 were higher (but not significantly different) in the egg stage than nestling stage for all nesting attempts and for nests without helpers. I found a statistically higher daily survival rate for nests in groups with helpers than in groups lacking helpers for the entire breeding season ($\chi^2 = 3.78$, df = 1, $P = 0.051$), egg stage ($\chi^2 = 2.78$, df = 1, $P = 0.096$), and nestling stage ($\chi^2 = 3.97$, df = 1, $P = 0.046$; Table 2).

I detected a significantly higher daily survival rate for nests with nestlings in 2002 versus 2003 for all nesting attempts ($\chi^2 = 3.34$, df = 1, $P = 0.068$; Table 2) and in 2002 for nests in the nestling stage of groups without helpers ($\chi^2 = 4.00$, df = 1, $P = 0.046$; Table 2).

DISCUSSION

The rate of abandonment of nests was low and for nests with video cameras was not different from nests monitored only by an observer (8 vs. 2%, respectively). The low level of abandonment indicates the cameras were

TABLE 2. Daily survival rate of nests (DSR) ± SE (* = significant *P*-value) (Mayfield analysis) for observer-monitored nests of Florida Scrub-jays on the Ocala National Forest, Florida, 2002–2003.

		Nest Daily Survival Rate (DSR) + SE (Exposure days)			χ^2, *P*
Year	Stage	All nesting attempts	Nests with helpers	Nests without helpers	Nests with helpers vs. non-helpers
2002	Entire season	0.979 ± 0.004 (1281)	0.989 ± 0.006 (267)	0.976 ± 0.005 (1014)	2.77, 0.096*
	Egg	0.956 ± 0.008 (617)	0.975 ± 0.014 (120)	0.952 ± 0.010 (497)	1.79, 0.181
	Nestling	0.959 ± 0.008 (664)	0.980 ± 0.012 (147)	0.954 ± 0.009 (517)	3.00, 0.083*
χ^2, *P*	Egg vs. nestling	0.07, 0.791	0.07, 0.786	0.02, 0.882	
2003	Entire season	0.971 ± 0.004 (1625)	0.979 ± 0.006 (623)	0.966 ± 0.006 (1002)	2.35, 0.126
	Egg	0.947 ± 0.008 (880)	0.960 ± 0.011 (328)	0.938 ± 0.010 (552)	2.19, 0.139
	Nestling	0.937 ± 0.009 (745)	0.956 ± 0.012 (295)	0.924 ± 0.012 (450)	3.56, 0.059*
χ^2, *P*	Egg vs. nestling	0.69, 0.406	0.06, 0.806	0.80, 0.370	
2000 and 2003	Entire season	0.975 ± 0.003 (2906)	0.982 ± 0.004 (890)	0.971 ± 0.004 (2016)	3.78, 0.051*
	Egg	0.951 ± 0.006 (1497)	0.964 ± 0.009 (448)	0.945 ± 0.007 (1049)	2.78, 0.096*
	Nestling	0.947 ± 0.006 (1409)	0.964 ± 0.009 (442)	0.940 ± 0.008 (967)	3.97, 0.046*
χ^2, *P*	Egg vs. nestling	0.222, 0.637	0.0, 1.00	0.221, 0.638	
χ^2, *P*	2002 vs. 2003-entire season	2.00, 0.157	1.39, 0.239	1.64, 0.200	
χ^2, *P*	2002 vs. 2003-egg	0.63, 0.426	0.71, 0.399	0.98, 0.322	
χ^2, *P*	2002 vs. 2003-nestling	3.34, 0.068*	2.00, 0.157	4.00, 0.046*	

readily accepted and did not affect the birds' nesting behavior.

Eastern coachwhip snakes are a known predator on Florida Scrub-jay nestlings (Westcott 1970, Schoech 1999). There is also evidence of nest predation by Red-tailed Hawk (*Buteo jamaicensis*), Eastern Screech-owl (*Otus asio*), Great Horned Owl (*Bubo virginianus*), Northern Harrier (*Circus cyaneus*), and bobcat (*Lynx rufus*); non-verified, but likely predators include the Swallow-tailed Kite (*Elanoides forficatus*), Fish Crow (*Corvus ossifragus*), Blue Jay (*Cyanocitta cristata*), and common raccoon (*Procyon lotor*) (Schaub et al. 1992). Swallow-tailed Kites have been observed trying to pluck nestlings from Florida Scrub-jay nests at the Archbold Station (S. J. Reynolds, pers. comm.). Hence, it is likely that scrub-jay nests are subjected to predation by other species in addition to those that I documented.

In my study, the observer visited within 15–20 m of the video-monitored nests to change the tape and battery every 2–3 days and did not visit the actual nest other than when the camera was deployed. It is possible that visits every 2–3 days may have provided additional clues for certain predators. Hence, the suite of predators might differ based on the different surveillance methods used.

The video camera results of my study (small sample sizes) indicated that predators took more nestlings than eggs. It may be that frequent visits by adults to feed the nestlings and the noise and/or movement produced by the young allow predators to more easily detect them than eggs. Woolfenden and Fitzpatrick (1984) found that nest predation affected the average number of fledglings produced per pair, overall nest success, and number of fledglings produced per breeding pair from successful nests.

The results of my study are similar to those of the wildland population studied by Bowman and Woolfenden (2001) as I found no difference in reproductive success between nests found in the egg stage compared to those found in the nestling stage. Further, the nest daily survival rates that I found indicated a nest had the same chance of surviving if it was in the egg stage as it did in the nestling stage when data for all nests, regardless of helper status, were pooled. The positive effect of helpers became even more obvious when data were pooled for 2002 and 2003. For example, no significant helper effect was evident in the egg stage for either 2002 or 2003, but was found when data for these years were pooled, likely the result of the larger sample size increasing the power of the statistical test (S. J. Zarnoch, pers. comm.). There was a significantly higher daily survival rate for nests with helpers in 2002 and 2003 during the nestling stage when data for both years were pooled. Daily survival rates were higher for nests of groups with helpers than for groups lacking helpers.

The daily nest survival rate data suggest that fledging rates likely would be higher in nests of groups with helpers. There was no difference in the number of eggs or the number of nestlings produced per breeding pair between nests with and without helpers. However, the number of fledglings per breeding pair was significantly higher (on average one-half fledgling) for pairs with helpers than in unassisted groups. Helpers had a positive effect on whether a nest would survive from one day to the next regardless of the stage of the nesting cycle. The daily nest survival rate data and the reproductive data support the conclusion that presence of helpers significantly increased the likelihood that a nest would survive and produce fledglings.

Predation pressure greatly affected reproductive success as 64% of the video-monitored nests had partial or complete predation. Given an equivalent level of loss in the observer-monitored nests, predation pressure would account for the relatively low reproductive success of only 1.71 fledglings per breeding pair in groups with no helpers and 2.24 fledglings per breeding pair in groups with helpers. Population management of this threatened species on the Ocala National Forest will likely require habitat management to increase the number of breeding territories and reduce the effectiveness of predator communities.

ACKNOWLEDGMENTS

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RED-COCKADED WOODPECKER FORAGING BEHAVIOR

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ABSTRACT.—We studied Red-cockaded Woodpeckers (*Picoides borealis*) to examine the effect of status and gender on foraging behavior. Foraging behavior of breeding pairs extended beyond separation by foraging height to include zones (bole, trunk in crown, primary limb, secondary limb) of the tree used and foraging methods (scaling, probing, excavating). Helper males and juvenile females maintained partial spatial separation from breeding adults. Helper males maintained spatial separation from breeding adults by exploiting limbs within tree crowns in both longleaf (*Pinus palustris*) and loblolly-shortleaf (*P. taeda*, *P. echinata*) pine forests, but also increased use of boles in loblolly-shortleaf pine in concert with reduced use of boles by adult females. Breeding males tended to forage less by scaling, probably due to the reduced proportion of foraging on boles of trees where scaling tends to predominate. *Received 29 June 2003. Accepted 31 August 2006.*

The genus *Picoides* is particularly rich in species that show behavioral differences in foraging niches. Details of niche separation have been described for most species in the genus including Downy Woodpecker (*P. pubescens*; Jackson 1970, Peters and Grubb 1983), Hairy Woodpecker (*P. villosus*; Kilham 1965), White-headed Woodpecker (*P. albolarvatus*; Ligon 1973), Three-toed Woodpecker (*P. tridactylus*; Hogstad 1976), Ladder-backed Woodpecker (*P. scalaris*; Austin 1976), Nuttall's Woodpecker (*P. nuttallii*; Jenkins 1979), and Red-cockaded Woodpecker (*P. borealis*; Ligon 1968). Behavioral differences in foraging niches in these studies generally involve differences in height and diameter of stems used, and in specific foraging methods. Grubb and Woodrey (1990) reviewed behavioral differences in foraging within species of *Picoides* woodpeckers and found no consistent patterns; behavior varied across species and geographically within species. Several hypotheses have been proposed to account for behavioral differences in foraging behavior within bird species including morphological specializations, size differences, social dominance, and reduction in competition for food resources (Selander 1966, Slatkin 1984)

The Red-cockaded Woodpecker is a cooperatively breeding species that lives in groups composed of breeding pairs and male helpers (Ligon 1970, Walters et al. 1988). Sexual dimorphism in size, although limited, has been detected (Pizzoni-Ardemani 1990). Behavioral differences in foraging behavior of Red-cockaded Woodpeckers have consistently been found when color-banded birds have been observed (Ligon 1970, Skorupa 1979, Ramey 1980, Hooper and Lennartz 1981). Females tend to forage lower on the tree (often on the bole) and males tend to forage higher. Because of the complex social system of Red-cockaded Woodpeckers, there is potential for status-based as well as gender-based differences in foraging behavior among individuals, unlike in other *Picoides* species. J. A. Jackson (pers. comm.) suggested that abundant midstory vegetation might force female Red-cockaded Woodpeckers into the foraging zone of males. He further suggested that females might suffer detrimental foraging impacts due to increased competition with presumably dominant males.

We examined the foraging biology of Red-cockaded Woodpeckers with particular emphasis on differences in foraging position and behavior of individuals differing in gender and social status. We hypothesized that Red-cockaded Woodpeckers might differ in foraging position and behavior, based not only on gender, but also on social status. We examined aspects of Jackson's hypothesis concerning shifts in foraging niche with presence of abundant midstory vegetation, and looked for evidence of male dominance maintaining niche separation between males and females.

METHODS

Study Area.—We observed foraging woodpeckers on the Angelina (31° 15′ N, 94°

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15′W) and Davy Crockett (31° 21′ N, 95° 07′ W) National forests in eastern Texas. Woodpecker habitats on the Davy Crockett National Forest and the northern portion of the Angelina National Forest are composed predominantly of loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines with a significant component of hardwoods, especially in the midstory. The southern portion of the Angelina National Forest is predominantly longleaf pine (*P. palustris*) with a minor hardwood component (Conner and Rudolph 1989).

Data Collection.—We banded Red-cockaded Woodpeckers (n = 42) present as regular members of 12 groups—six in longleaf pine forest and six in loblolly-shortleaf pine forest—with a federal band on one leg, and two color bands on the other leg. We began adding a white band to the leg with the federal band later in the study to facilitate reading bands in the field. Capture and banding of woodpeckers was initiated in late summer, which allowed us to identify juveniles prior to the post-juvenile molt (Jackson 1979). Band combinations were identified using binoculars or a 20X spotting scope during foraging observations.

Individual birds were assigned to one of six social status categories. The breeding male was the adult male roosting in the nest cavity, the breeding female was the only adult female present prior to the breeding season, and helper males and females were all non-breeding adults, with the exception of the breeding pair, in excess of 1 year of age. Juveniles were individuals less that 1 year of age, even though they had attained adult plumage.

We obtained foraging observations during 1–5 days for each of the 12 groups. Numbers of observations were fairly evenly split between two periods; 29 August to 2 November 1989 (57%), and 28 December to 19 February 1989–90 (43%). Ten groups were observed for either 4 or 5 days, and no group was observed for more than 1 day in any given month. Contact was initiated each day as woodpeckers exited roost cavities shortly after dawn. We attempted to maintain contact with each group for approximately 3 hrs. This was usually accomplished, although we occasionally lost contact for up to 45 min. This generally coincided with a period of intense foraging. Foraging is interspersed with other activities later in the day (i.e., cavity maintenance, loafing) and we did not examine foraging behavior at these times.

We needed to obtain data simultaneously on two or more individuals to obtain foraging data when positions of individuals relative to others in the group were known. This precluded methods commonly used to avoid biases, such as taking samples at set time intervals or at a set time after an individual was located. A minimum of 10 min was maintained between observations to minimize lack of independence between successive samples. The same two observers, working as a team, attempted to identify and track individuals. We initiated data collection when two or more woodpeckers were simultaneously identified. We collected data for single individuals if we were experiencing difficulty identifying multiple individuals. Identification of pairs without helpers or juveniles was much easier and, consequently, data accumulated more rapidly for pairs than for larger groups. We recorded time and location within the home range, foraging method (scaling, probing, excavating, other), foraging zone (bole, trunk in crown, primary limb, secondary limb, other), diameter of stem at foraging site, height of foraging site above ground, and total tree height for each individual woodpecker. The condition of the foraging substrate was recorded as (1) live, (2) dead portion of live tree, (3) dying tree, or (4) dead tree. Diameter of the stem at the foraging position was visually estimated using the known dimensions of the woodpecker as a gauge; heights (m) were estimated using a clinometer.

Foraging tree species, tree diameter at breast height (DBH) and canopy height, and distances between any multiple trees involved in simultaneous foraging observations were recorded after foraging observations were terminated for the day. We calculated standardized foraging heights as a percent (foraging height/tree height × 100) of total tree height for each foraging observation.

Data Analysis.—Data were combined for the late August through mid-February period to obtain an adequate sample size. We used a two-way factorial ANOVA with Bonferroni's MRT to investigate the relationships among forest type (loblolly-shortleaf, longleaf), bird status, and bird foraging locations (foraging height, standardized foraging height, stem diameter, tree height, tree DBH, and canopy height). We looked for differences among bird status categories within forest types if there was a significant interaction ($P \leq 0.10$) between forest type and bird status. Statistical significance of remaining tests was set at $P < 0.05$.

Observation periods when only the breeding male and breeding female were present were used to explore dominance of breeding males in relation to foraging position of breeding females. Pairs either shared a tree or foraged in different trees. Vertical separation was calculated as breeding male foraging height minus breeding female foraging height. Two-way factorial ANOVA was used to examine effects of forest type and sharing of trees on vertical separation.

We used three-way tests of independence (G) to examine the relationships among forest types, bird status, and behaviors (foraging zone, foraging substrate, and foraging method; Sokal and Rohlf 1995:737–759). Forest type, bird status, and foraging zone ($G = 114.18$, df = 24, $P < 0.001$), foraging substrate ($G = 80.69$, df = 17, $P < 0.001$), and foraging method ($G = 66.01$, df = 17, $P < 0.001$) were not independent. Therefore, we conducted two-way tests of independence between bird status and foraging behavior within each forest type. We used simultaneous test procedures (STP, Sokal and Rohlf 1995:722–724) to examine which bird status categories differed.

RESULTS

Red-cockaded Woodpecker groups for which foraging data were obtained consisted of pairs ($n = 3$, 2 in longleaf and 1 in loblolly-shortleaf) and pairs with 1–3 helpers and/or juveniles ($n = 9$). Breeding males were assumed to be those individuals roosting in the 1989 nest cavity and their identities were confirmed during the 1990 breeding season. Breeding females were the only adult-plumaged females present at the time of initial banding. All remaining adult-plumaged males (late summer) were designated as helpers. Group membership was highly stable during the duration of the study, with only the replacement of a breeding female and the disappearance of one juvenile female.

We logged 125 contact hrs during the data collection period. Data were obtained on 42 individual birds on 460 separate occasions. We recorded 946 individual foraging observations, 512 in longleaf pine and 448 in loblolly-shortleaf pine. Of the 946 observations, 7% involved single birds, 64% involved two birds, and 28% involved three or more birds.

General Foraging Behavior.—Red-cockaded Woodpecker group members aggregated in the general vicinity of the roost trees, usually at the roost tree of the breeding male, after exiting roost cavities. An extended period of foraging ensued after a brief period of social interaction. This usually lasted throughout our approximately 3-hr observation period. Foraging was occasionally interrupted by work on cavities or resin wells, and interactions with neighboring groups.

Foraging was predominantly on pines (94.2%). Limited foraging (5.8%) occurred on eight species of hardwoods, primarily oaks (*Quercus* spp.). Various arthropods were the primary object of foraging activities. The major exception observed was foraging for seeds from longleaf pine cones. This behavior was recorded six times during foraging observations and an additional 49 times during periods between observations. All observations of foraging on seeds were between late October and early January, most in early November. This period corresponds to the opening of longleaf pine cones and dispersal of seeds. Red-cockaded Woodpeckers typically perched on an open cone, removed the seed, and flew to the bole or large limb of the pine. The seed and attached wing were wedged between the stem and the breast feathers, the wing was removed by pecking, and the seed was consumed. Red-cockaded Woodpeckers were not observed to feed on available seeds of loblolly or shortleaf pines. They also extracted tip moth larvae (*Dioryctria* sp.) from green longleaf pine cones (12 times during Aug and Oct) and flycatching behavior was observed twice.

Woodpecker groups foraged extensively on pines dying of southern pine beetle (*Dendroctonus frontalis*) and engraver beetle (*Ips* spp.) infestation when these were available. Red-cockaded Woodpeckers foraged on dead and dying pine-bark-beetle-infested trees during 9.3 and 13.4% of the observations, respectively, in longleaf and loblolly-shortleaf pine habitats. Trees infested by pine bark beetles did not preferentially attract the attention of foraging Red-cockaded Woodpeckers early in the beetle's developmental cycle. Eggs and larvae are present at the depth of the vascular cambium at this time, but were not excavated by Red-cockaded Woodpeckers. Infested trees began to be preferentially visited only late in the infestation cycle after pupae and callow adults were present within the outer layers of bark. The pines were essentially dead at this point with all needles reddish and drying. Red-cockaded and other woodpeckers often completely stripped the outer layers of bark from the infested portions of the bole to expose the beetles. Slightly later in the cycle, more substantial excavations were directed at arthropods involved in secondary infestations of the beetle-killed pines. Red-cockaded Woodpeckers greatly curtailed their foraging activities on infested trees when substantial shedding of dead needles and loosening of the bark commenced.

Red-cockaded Woodpeckers appeared to obtain prey items more frequently, and secured items of larger average size, when foraging on trees infested by southern pine beetles. Groups often moved directly to infested trees early in the morning. Typically, all group members foraged together in the infested tree(s) for substantial periods. The mean time individual Red-cockaded Woodpeckers foraged on a southern-pine-beetle-infested tree was 21.3 min ($n = 68$), compared with a mean of 6.8 min for a randomly selected sample of living trees ($n = 50$).

Foraging Behavior in Relation to Gender, Age, and Social Status.—Sample sizes for helper females (zero in longleaf pine and 14 in loblolly-shortleaf pine) and juvenile males (28–30 in longleaf pine and 3 in loblolly-shortleaf pine) were too small to be considered representative of the bird status category and were deleted from analyses. The cone foraging method was dropped from analyses because it was used only in longleaf pine forest and was restricted to a limited time period.

Foraging and Tree Measures.—There were no interactions among forest type, bird status category, and foraging location for tree DBH ($F = 0.86$, $P = 0.46$) and canopy height ($F = 2.05$, $P = 0.11$). Tree DBH was similar in both forest types ($F = 1.86$, $P = 0.17$) and across all bird status categories ($F = 0.87$, $P = 0.46$; mean = 40 cm, SE = 0.41). Canopy height was greater in loblolly-shortleaf pine forest than in longleaf pine forest (26 m, SE = 0.2 vs. 25 m, SE = 0.1; $F = 31.84$, $P < 0.001$), but did not differ ($F = 1.30$, $P = 0.27$) among bird status categories.

Interactions occurred among forest type, bird status category, and foraging location for stem diameter ($F = 2.22$, $P = 0.084$) and height of tree ($F = 3.53$, $P = 0.015$). Diameter of stems within both forest types differed among bird status categories ($P < 0.001$; Fig. 1A). Breeding and helper males in longleaf pine forest foraged on significantly smaller diameter stems than breeding and juvenile females. Breeding males in loblolly-shortleaf pine forest also foraged on significantly smaller diameter stems than breeding and juvenile females. However, helper males were observed on larger stems, similar in diameter to those used by both females and breeding males.

Height of tree in loblolly-shortleaf pine forest did not differ among bird status categories (mean = 26 m, SE = 0.2; $F = 0.58$, $P = 0.63$). However, in longleaf pine forest, height of tree differed among bird status categories ($F = 6.63$, $P < 0.001$); helper males foraged in shorter trees (22 m, SE = 0.7) than other bird status categories (25 m, SE = 0.2; Fig. 1B).

Foraging and Bird Location.—There was no interaction between forest type and bird status category for woodpecker foraging height ($F = 0.22$, $P = 0.89$). However, when foraging height was standardized by height of tree, the interaction was significant ($F = 4.28$, $P = 0.005$). Overall, woodpeckers foraged at greater heights in loblolly-shortleaf pine forest than in longleaf pine forest (20 m, SE = 0.3 vs. 17 m, SE = 0.3, $F = 32.97$, $P < 0.001$). Foraging heights differed between breeding males and breeding females with forest types combined due to lack of interaction ($F = 11.64$, $P < 0.001$); breeding males foraged higher in the tree than breeding females (20 m, SE = 0.3 vs. 17 m, SE = 0.3) (Fig. 1C).

The difference in standardized foraging heights of males and females in longleaf pine was pronounced ($F = 11.14$, $P < 0.001$, Fig. 1D) when foraging height was standardized by height of tree. Breeding males also had a

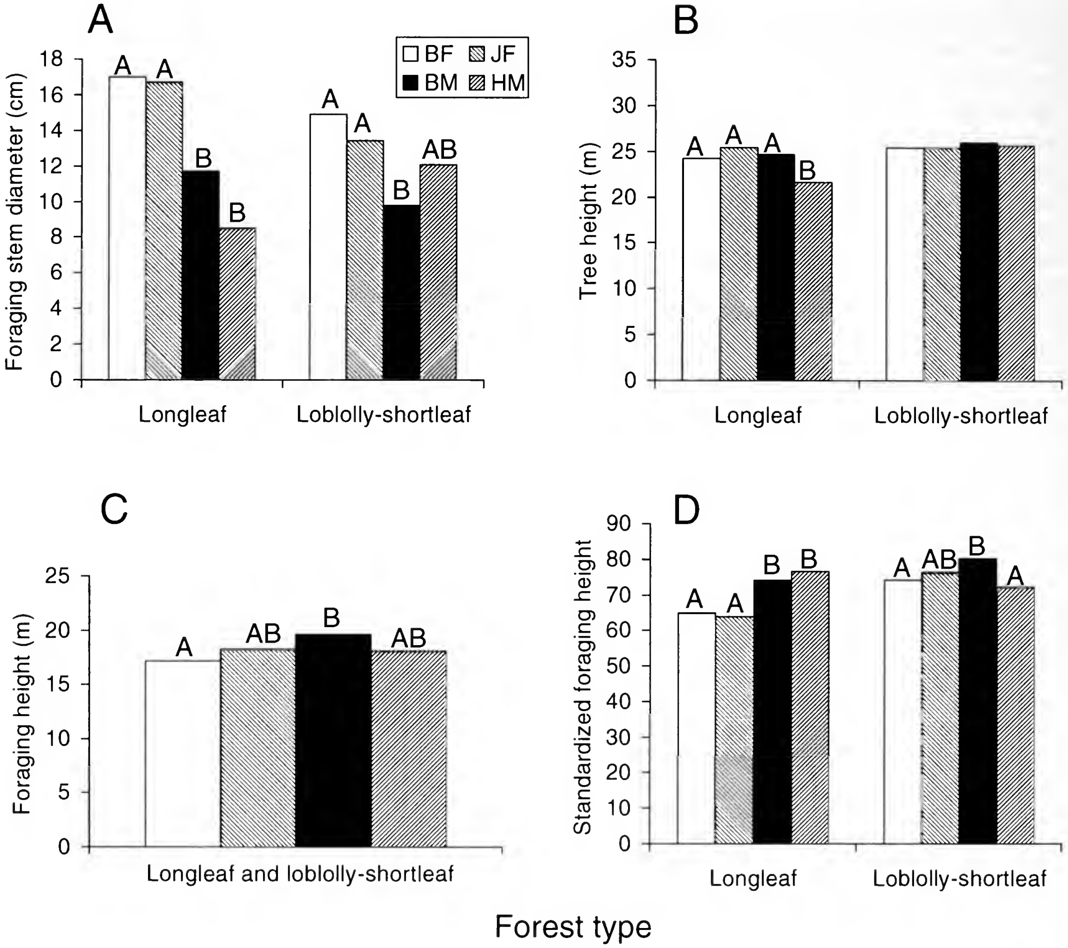

FIG. 1. Red-cockaded Woodpecker foraging stem diameters (A), foraging tree heights (B), foraging heights (C), and standardized foraging heights (D) in longleaf and loblolly-shortleaf pine habitats in eastern Texas, 1989–90 (BF = breeding females, longleaf n = 192–206 and loblolly-shortleaf n = 150–153; BM = breeding males, longleaf n = 174–182 and loblolly-shortleaf n = 139–141; HM = helper males, longleaf n = 24–26 and loblolly-shortleaf n = 41; and JF = juvenile females, longleaf n = 50–51 and loblolly-shortleaf n = 72–73). Different letters above bars indicate differences ($P < 0.05$) between birds of different status within forest types.

greater standardized foraging height than breeding females in loblolly-shortleaf pine forest ($F = 6.83$, $P < 0.001$).

There was no interaction between forest type and sharing of trees for vertical separation of breeding males and breeding females ($P = 0.18$). Pairs in different trees ($n = 110$) were spaced farther apart vertically than pairs in the same tree ($n = 68$) (4.4 vs. 3.0 m, $P = 0.012$). Vertical separation of pairs was greater in longleaf pine forest than in loblolly-shortleaf pine forest (4.4 vs. 2.8 m, $P = 0.006$).

Bird status and frequency of foraging by zone within the tree were not independent in longleaf ($G = 46.29$, df = 9, $P < 0.001$) or loblolly-shortleaf pine forest ($G = 47.87$, df = 9, $P < 0.001$), (Fig. 2A, B). Breeding males and helper males in longleaf pine forest had similar distributions among zones within the tree; breeding females and juvenile females were also similar (Fig. 2A). Helper males in loblolly-shortleaf pine forest were more similar to breeding females and juvenile females (Fig. 2B) due primarily to increased foraging on the boles of trees.

At least one member of the breeding pair

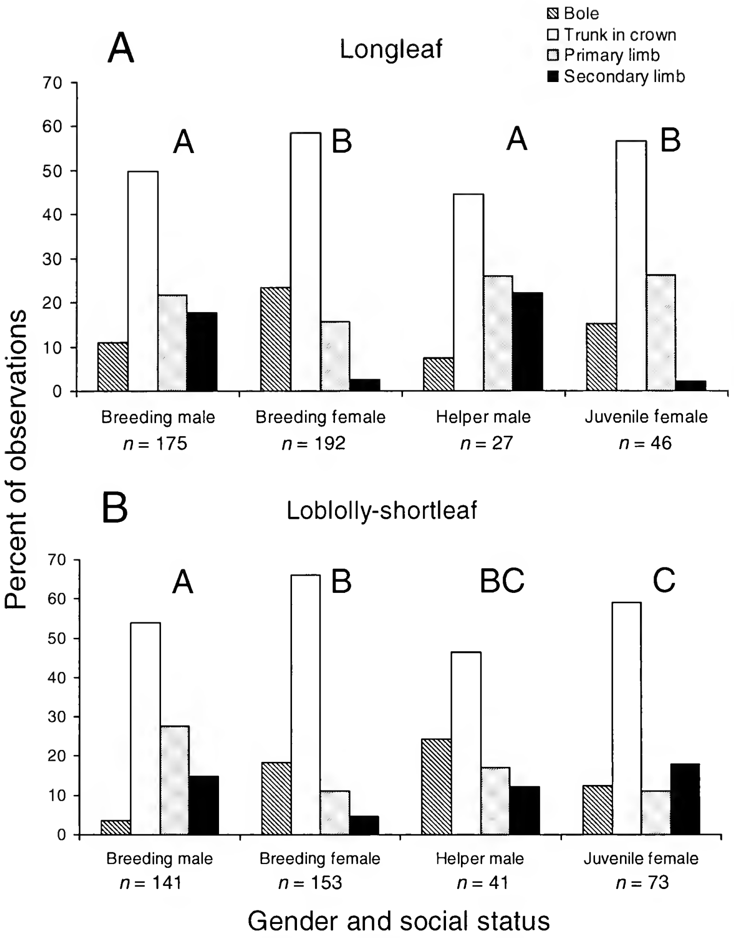

FIG. 2. Red-cockaded Woodpecker foraging frequencies by tree zone in longleaf (A) and loblolly-shortleaf (B) pine habitats in eastern Texas, 1989–90. Different letters above distributions of bird types indicate differences ($P < 0.05$) within forest types.

was present in the same tree when helper males foraged on the boles of trees ($n = 7$) in loblolly-shortleaf forest. In contrast, when helper males foraged in other zones within the tree, at least one member of the breeding pair was present in the same tree during only 47% of the observations ($n = 19$).

Bird status and use of foraging substrate in longleaf pine forest were not independent ($G = 34.75$, df = 6, $P < 0.001$), (Fig. 3A). Breeding males and helper males had similar distributions among substrates; breeding females and juvenile females were also similar. Bird status and use of foraging substrate were independent ($G = 12.29$, df = 6, $P = 0.056$; Fig. 3B) in loblolly-shortleaf pine forest.

Foraging Method.—Bird status and foraging method in longleaf pine forest were independent ($G = 9.46$, df = 6, $P = 0.15$), implying that foraging methods did not differ by gender and social status (Fig. 4A). In contrast, bird status and foraging method were not independent ($G = 42.11$, df = 6, $P < 0.001$) in loblolly-shortleaf pine forest (Fig. 4B). The proportion of time spent using different foraging methods was similar for breeding males and breeding females, whereas helper males were similar to breeding females, but differed from breeding males.

DISCUSSION

The differences we noted between forest types resulted primarily from differences in forest structure and tree species. Greater hard-

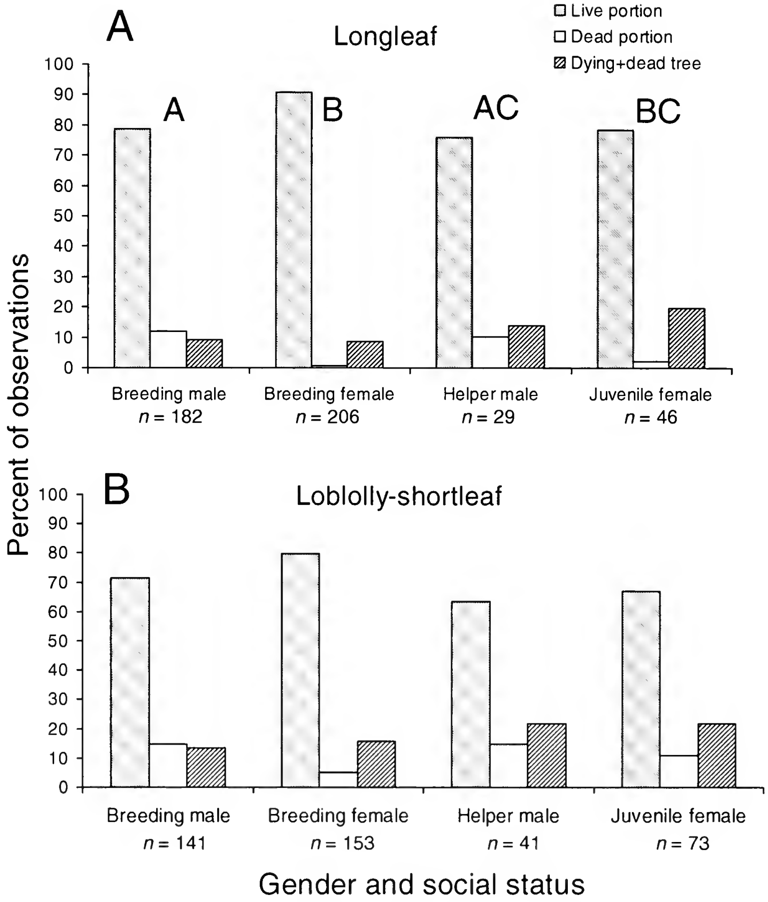

FIG. 3. Red-cockaded Woodpecker foraging frequencies by tree substrate in longleaf (A) and loblolly-shortleaf (B) pine habitats in eastern Texas, 1989–90. Different letters above distributions of bird types indicate differences ($P < 0.05$) within forest types.

wood midstory in loblolly-shortleaf pine forest was associated with greater foraging heights in pines, especially for females (Rudolph et al. 2002). The generally greater abundance of hardwoods in loblolly-shortleaf pine forest was also associated with consistently greater use of hardwoods for foraging than in longleaf pine forest (Rudolph et al. 2002).

Dead and dying pines composed a greater proportion of Red-cockaded Woodpecker foraging sites than previously reported (Ligon 1970, Baker 1971, Nesbitt et al. 1978, Hooper and Lennartz 1981). This is almost certainly due to the generally high southern pine beetle populations in eastern Texas (Hedden 1978, Price and Doggett 1978). Greater use of bark beetle infested pines in loblolly-shortleaf pine habitats compared to longleaf pine habitats was presumably due to the greater prevalence of southern pine beetle infestations in the more susceptible loblolly and shortleaf pines (Hodges et al. 1979).

Use of pine seeds was restricted to longleaf pine (Ramey 1980, Hooper and Lennartz 1981, this study), as was the excavation of green cones to obtain arthropod prey. Hooper and Lennartz (1981) noted that foraging birds perched directly on the cones and hypothesized the larger size of longleaf pine cones may have influenced their use. However, larger size and nutritional benefit of longleaf pine seeds may be the primary factor. The average weight of longleaf pine seeds is approximately 93 mg versus 25 mg for loblolly pine and 9.8 mg for shortleaf pine (Schopmeyer 1974). Excavation on cones was also restricted to long-

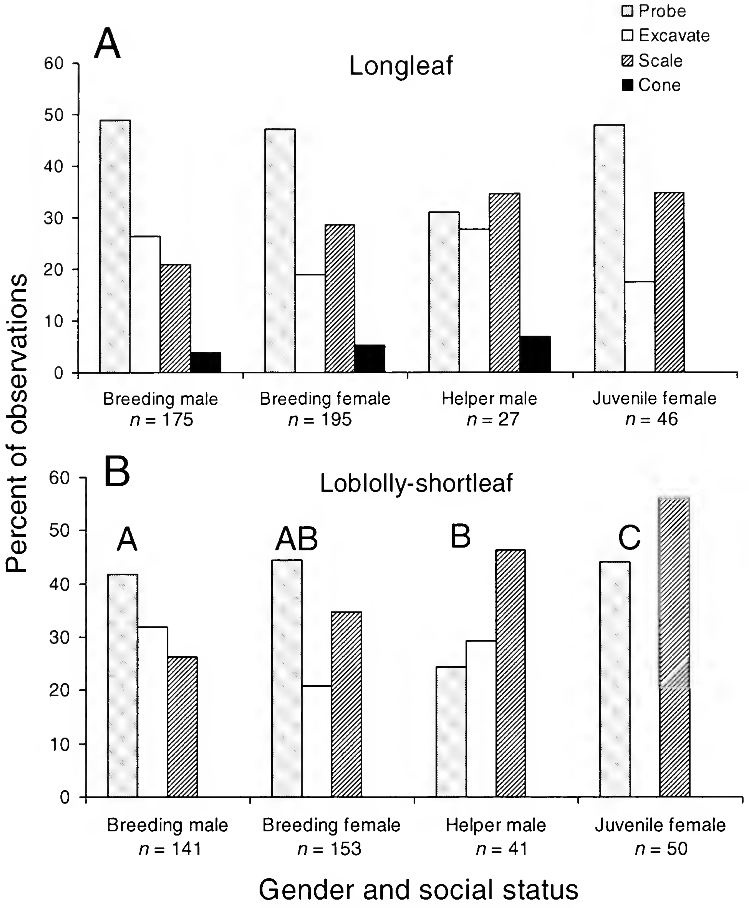

FIG. 4. Foraging frequencies of Red-cockaded Woodpeckers by foraging method in longleaf (A) and loblolly-shortleaf (B) pine habitats in eastern Texas, 1989–90. Different letters above distributions of bird types indicate differences ($P < 0.05$) within forest types.

leaf pines. Birds appeared to be excavating for tip moth larvae in both Texas (this study) and South Carolina (Hooper and Lennartz 1981).

All members of social groups typically forage together, which limits the potential for differential use of overall habitat, or even individual trees, by birds of different social status or age. We found no significant differences in overall habitat or tree characteristics (tree height, tree DBH, canopy height) among birds of different social status or age, with one exception. Helper males in longleaf pine habitat foraged in shorter trees than did other social classes of Red-cockaded Woodpeckers.

Ligon (1968) first reported behavioral differences in foraging behavior in Red-cockaded Woodpeckers. Males were observed to forage mainly on limbs and upper trunks, while females foraged mainly on upper and especially lower trunks. Similar results, differing only in minor details, have been reported in subsequent studies (Skorupa 1979, Ramey 1980, Hooper and Lennartz 1981). Studies that have not detected gender differences have failed to present data (Beckett 1971), or did not involve marked birds (Morse 1972, Miller 1978).

Our results confirmed the general pattern of spatial separation of male and female Red-cockaded Woodpeckers. However, additional differences between birds of differing age and social class were also found. In longleaf pine forest, breeding and helper males foraged at greater heights than females, especially if standardized foraging heights were considered. A similar pattern occurred in loblolly-shortleaf pine forest for breeding males and females, but at greater absolute heights, presumably due to greater canopy heights and the restriction of foraging space. Helper males foraged at significantly lower standardized heights due to increased foraging on the boles of pines. The well-developed midstory in this forest type may constrain foraging to lower levels, especially for females.

Significant differences were consistently found between breeding males and breeding females in relation to foraging stem diameters, zone within the tree, and foraging substrate in both forest types. Breeding males exhibited a greater propensity to forage on smaller diameter stems, more often on branches and less often on boles, and more often on dead portions of living trees consisting of self-pruning limbs, compared to breeding females. Each of these differences is consistent with the vertical separation maintained between breeding males and breeding females.

Juvenile females were intermediate between breeder classes and resembled breeding females for these measures. The pattern is more complex for helper males. Helper males closely resembled breeding males in longleaf pine forest. However, helper males in loblolly-shortleaf forest differed significantly from breeding males in relation to zones used within the tree, more closely resembling breeding females. This was a result of greater use of tree boles by helper males. This results in a reversal of the pattern of foraging stem diameters used by helper males compared with breeding males; helper males used larger stems in loblolly-shortleaf pine forest and smaller stems in longleaf pine forest.

Our results confirm the tendency for gender separation of foraging position reported in previous studies (Ligon 1968, Hooper and Lennartz 1981). Our data suggest that helper males maintain some separation in foraging position from breeding adults. Breeding adult males and females concentrate much of their foraging activities on the trunk in the crown. Secondarily, breeding males use limbs and breeding females use boles to a greater extent than the other gender. Helper males are similar to breeding males in their general choice of foraging position, but show a consistent tendency to shift from the foraging niche of breeding males. Helper males in longleaf pine forest forage to a greater extent on primary and secondary branches and less on boles than breeding males. However, helper males in loblolly-shortleaf pine forest also increased foraging on boles of pines, contrary to the situation in longleaf forest. This may be a result of the reduced use of boles by breeding females in loblolly-shortleaf pine forest, presumably due to the greater amount of hardwood midstory vegetation compared to longleaf habitats. Concurrent observations (Rudolph et al. 2002) suggest that Red-cockaded Woodpeckers tend to avoid foraging in situations with dense midstory vegetation.

The foraging positions and behaviors of breeding male and female Red-cockaded Woodpeckers are consistent with the assumed social dominance of breeding males (Ligon 1970) and limited dimorphism (Pizzoni-Ardemani 1990). We suspect that social dominance is the mechanism driving differential foraging positions, but clearly more information is required concerning this aspect of foraging. Red-cockaded Woodpeckers exhibit some plasticity in foraging behavior due to habitat (i.e., encroaching midstory; Rudolph et al. 2002, this paper). The behavior of helper males is more complex, suggesting reduction in competition among group members may also be involved. Helper males in longleaf pine forest foraged in portions of trees most similar to that of the breeding male, maintaining significant spatial separation. However, in loblolly-shortleaf pine forest where encroaching midstory resulted in more intense foraging by the breeding pair in tree crowns, consistent with Jackson's (pers. comm.) hypothesis, helper males also increased foraging on tree boles that were partially vacated by breeding females. This observation suggests that morphological differences between males and females do not completely constrain foraging position.

Social dominance and reduction in competition for prey appear to be important, although overt aggression was rarely observed among established group members, especially between members of the breeding pair. Hooper and Lennartz (1981) reported a similar lack of conflict between adult group members. This lack of aggression is expected in these typically well-established social groups. Regardless of the mechanisms controlling foraging behaviors, Red-cockaded Woodpeckers maintain a sophisticated separation of foraging space in relation to gender and social status.

The observed foraging behavior of Red-cockaded Woodpeckers in eastern Texas differed between loblolly-shortleaf and longleaf pine habitats. The observed differences were presumably related to differences in vegetation structure (amount of midstory vegetation), bark beetle abundance, and pine species. Differences between Red-cockaded Woodpeckers of differing gender, age, and social status were detected for several aspects of foraging behavior. These results are consistent with the frequent pattern of gender variation in foraging behavior within the genus *Picoides*. The occurrence of cooperative breeding and consequent existence of larger social groups, which frequently remain intact for several years (Walters et al. 1988), presumably allows for development of more complex partitioning of the foraging niche in this cooperatively breeding species.

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VARIATION IN REPRODUCTIVE INDICES IN THREE POPULATIONS OF COOPER'S HAWKS

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ABSTRACT.—We investigated several reproductive attributes among three spatially and morphometrically separable northern populations of breeding Cooper's Hawks (*Accipiter cooperii*) in differing ecological settings in British Columbia, North Dakota, and Wisconsin during 1995–2001. We did not detect significant inter-year variation in reproduction within any of our study areas. Cumulative clutch and brood sizes were significantly higher in British Columbia (mean = 4.41 and 3.60, respectively) and Wisconsin (4.26 and 3.73) than in North Dakota (3.5 and 3.0), but not significantly different between British Columbia and Wisconsin. Total nest success rates (91 and 82% in British Columbia and Wisconsin, respectively) varied significantly among all three study sites, but were lowest in North Dakota (68%). We hypothesize that smaller clutch and consequentially lower brood sizes in North Dakota may be the result of the comparatively later nesting phenology in this highly migratory population. Our results underscore the significance of clutch size data, and the need for further research on regional and other large-scale variation in avian demographic parameters to help decide if, when, and where population demographics may warrant a management response. *Received 22 July 2006. Accepted 11 September 2006.*

Comparative studies of different populations of widespread species can help identify local and/or regional selective forces that produce geographic variation in life histories and population dynamics (Kroodsma and James 1994, Martin 2004). Recent evidence indicates the Cooper's Hawk (*Accipiter cooperii*) can nest successfully in a wide array of wooded or semi-wooded habitats in some areas of its broad North American range (Wiggers and Kritz 1991; Rosenfield et al. 1995; Boal and Mannan 1998; Nenneman et al. 2002, 2003). However, there is concern for the long-term viability of Cooper's Hawk populations in some areas because it is perceived as an area-sensitive, forest-interior species (e.g., Freemark and Collins 1992, Bosakowski et al. 1993, Kirk 1996, Kirk and Hyslop 1998, Grant and Berkey 1999). Further, some habitats may serve as reproductive sinks for this species (Boal and Mannan 1999, Roth et al. 2005), and some authors have suggested declines in eastern populations of Cooper's Hawks (Meehan et al. 2001). Trichomoniasis and West Nile virus (WNV) also have the potential to adversely influence Cooper's Hawk breeding populations (Boal and Mannan 1998, Wünschmann et al. 2004; but see Rosenfield et al. 2002b and Stout et al. 2005). The prevalence of these diseases is poorly documented across the vast breeding range of the Cooper's Hawk and additional studies are needed to examine the risks and population effects of WNV exposure (Stout et al. 2007).

The Cooper's Hawk is listed as threatened or as a species of special concern in some eastern and Midwestern states (including North Dakota among our study sites), usually without support of demographic data (Rosenfield and Bielefeldt 1993, Nenneman et al. 2002). Kirk and Hyslop (1998) observed that demographic data, including productivity data, are too few and inadequate for assessing population status of accipiters in Canada. Fuller (1996) also noted the scarcity of population data for accipiters in North America and emphasized the need for basic ecological information to benefit conservation assessments

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for populations that are presumably adapted to local and/or regional habitats.

Breeding Cooper's Hawks among our study sites in British Columbia, North Dakota, and Wisconsin are morphometrically separable based on body mass, wing chord, and other mensural attributes (Rosenfield et al. 2003, Rosenfield 2006). There is no evidence that suggests movement of breeding birds among these three populations (Rosenfield 2006)

The objectives of our study are to: (1) compare reproductive indices among three spatially and morphometrically separate populations and (2) identify ecological factors that might lead to differing reproductive attributes in northern populations of a continentally widespread species.

METHODS

Study Sites.—We studied three northern populations of breeding Cooper's Hawks at similar latitudes (44–48° N) on Vancouver Island in coastal British Columbia, western North Dakota, and southern Wisconsin. Study sites have a longitudinal span of 2,700 km in the northern United States and southwestern Canada near the northern edge of this species' nesting range (Rosenfield and Bielefeldt 1993). The British Columbia site is in sparsely to wooded habitat in and near Victoria, which exhibits a temperate, coastal climate and is dominated by tall coniferous trees (Douglas-fir [*Pseudotsuga menziesii*] and grand fir [*Abies grandis*]; Campbell et al. 1990). The North Dakota site is a grassland and cropland landscape with scattered small, highly fragmented woodlands including green ash (*Fraxinus pensylvanica*), trembling aspen (*Populus tremuloides*), and boxelder (*Acer negundo*) of relatively small stature as prominent tree species (Murphy 1993, Nenneman et al. 2002, Rosenfield et al. 2002a). The southern Wisconsin landscape has moderate amounts of forest cover dominated by oaks (*Quercus* spp.) and pines (*Pinus* spp.) (Curtis 1959, Trexel et al. 1999). Both North Dakota and Wisconsin experience highly seasonal, mid-continental climates. Predominant vegetation, potential nest sites, and other landscape and climatological features present striking differences in the ecological settings of these three study sites.

All nests on all three study sites were objectively discovered by searching woodland habitats without foreknowledge or preconception of the presence of nesting hawks (Stewart et al. 1996, Bielefeldt et al. 1998, Trexel et al. 1999, Rosenfield et al. 2002a, Nenneman et al. 2003). All nests on all three study sites were found at comparable times before laying began or during the earliest stages of incubation (≤10 days) as described by Stewart et al. (1996) and in Rosenfield et al. (2000, 2002a). Clutch size was ascertained by climbing to nests near the midpoint (~15 days) of an incubation period that spans ~34 days (Rosenfield and Bielefeldt 1993). We again climbed to nests when young were ~18 days of nestling age (or 70% of fledging age [i.e., 25 days]) to band young and derive brood size (Rosenfield and Bielefeldt 2006, Stout et al. 2007). The data were pooled with counts of young in other occupied nests (i.e., eggs laid; Steenhof 1987) for which we did not have clutch counts. Visits to nests when young are 70% of fledging age are within the range of ages recommended for safe handling and banding of nestling raptors (Fyfe and Olendorff 1976). This avoids the 80% of fledging age metric suggested by Steenhof (1987) that could result in premature fledging of some nestlings and/or obtaining inaccurate counts of young (Rosenfield et al. 2007). We considered all occupied nests to be successful if at least one nestling reached ≥18 days of age following Stout et al. (2007). Nest success was the proportion of occupied nests that were successful. Unsuccessful nests were included in our analyses as producing zero young for calculation of brood size per occupied nest. We adopted the format of others and present brood counts by occupied and successful nest categories (Rosenfield and Bielefeldt 1993, Stout et al. 2007). Studies were conducted concurrently on all sites in 1995–2000, and (for brood size only) in 2001.

Non-parametric procedures were used where appropriate (e.g., small sample sizes and proportions) and all statistical procedures and tests follow Stout et al. (2007) and Zar (1999). We calculated probability values of parametric and non-parametric tests using SYSTAT (Wilkinson 1992) and StatXact-Turbo (Mehta and Patel 1992), respectively. Significance was accepted at $P \leq 0.05$. We report means ± SE except where noted.

TABLE 1. Reproductive characteristics [mean ± SE (*n*)] for Cooper's Hawks in British Columbia (BC), North Dakota (ND), and Wisconsin (WI), 1995–2001.

	Study area		
Parameter/Year	BC	ND	WI
Clutch size[a]			
1995	5.00 ± 0.00 (3)	4.00 ± 0.00 (2)	4.00 ± 0.19 (21)
1996	4.21 ± 0.18 (28)	3.31 ± 0.25 (16)	3.94 ± 0.16 (18)
1998	4.35 ± 0.15 (31)	3.71 ± 0.18 (7)	4.35 ± 0.13 (23)
1999	5.00 ± 0.19 (8)	4.00 ± 0.00 (3)	4.40 ± 0.17 (20)
2000	4.60 ± 0.24 (5)	3.00 ± 0.71 (4)	4.52 ± 0.13 (21)
All years[b]	4.41 ± 0.09 (75)^{D}	3.50 ± 0.15 (32)^{E}	4.26 ± 0.07 (103)^{D}
Brood size			
1995	[c]3.73 ± 0.30 (15)	1.69 ± 0.47 (16)	2.83 ± 0.29 (35)
	[d]4.00 ± 0.15 (14)	3.37 ± 0.37 (8)	3.52 ± 0.22 (29)
	[e]93% (15)	50% (16)	83% (35)
1996	[c]3.35 ± 0.29 (29)	2.46 ± 0.28 (26)	3.12 ± 0.28 (33)
	[d]3.59 ± 0.25 (27)	3.05 ± 0.19 (21)	3.64 ± 0.17 (28)
	[e]93% (29)	81% (26)	85% (33)
1998	[c]3.19 ± 0.22 (32)	1.88 ± 0.34 (16)	3.19 ± 0.36 (27)
	[d]3.29 ± 0.19 (31)	2.50 ± 0.26 (12)	4.14 ± 0.19 (21)
	[e]97% (32)	75% (16)	78% (27)
1999	[c]3.06 ± 0.30 (31)	2.00 ± 0.46 (15)	3.25 ± 0.29 (28)
	[d]3.52 ± 0.24 (27)	3.33 ± 0.24 (9)	3.79 ± 0.17 (24)
	[e]87% (31)	60% (15)	86% (28)
2000	[c]3.33 ± 0.29 (27)	1.92 ± 0.31 (24)	2.88 ± 0.37 (25)
	[d]3.75 ± 0.25 (24)	2.71 ± 0.24 (17)	3.53 ± 0.36 (19)
	[e]89% (27)	71% (24)	76% (25)
2001	[c]3.33 ± 0.32 (27)	2.15 ± 0.38 (20)	3.29 ± 0.41 (17)
	[d]3.75 ± 0.25 (24)	3.31 ± 0.17 (13)	3.53 ± 0.36 (15)
	[e]89% (27)	65% (20)	88% (17)
All years[b]	[c]3.29 ± 0.12 (161)^{D}	2.05 ± 0.15 (117)^{E}	3.07 ± 0.13 (165)^{D}
	[d]3.60 ± 0.09 (147)^{D}	3.00 ± 0.10 (80)^{E}	3.73 ± 0.09 (136)^{D}
	[e]91% (161)^{D}	68% (117)^{E}	82% (165)^{F}

[a] There were no significant inter-year differences in clutch size within British Columbia (Kruskal-Wallis test, $H = 7.941$, df = 5, $P = 0.09$), North Dakota (Kruskal-Wallis test, $H = 4.304$, df = 5, $P = 0.29$), or Wisconsin (ANOVA, $F_{4,98} = 2.231$, $P = 0.07$). Variation in brood size among study years for occupied and successful nests did not differ within British Columbia (ANOVA, $F_{5,155} = 0.7$, $P = 0.81$, occupied nests; ANOVA, $F_{5,141} = 0.99$, $P = 0.42$, successful nests), North Dakota (ANOVA, $F_{5,111} = 0.599$, $P = 0.59$; ANOVA, $F_{5,74} = 2.08$, $P = 0.08$), and Wisconsin (ANOVA, $F_{5,159} = 0.348$, $P = 0.88$; ANOVA, $F_{5,130} = 1.12$, $P = 0.36$). There was no significant inter-year variation in nest success rates within British Columbia (Fisher statistic = 2.73, df = 5, $P = 0.74$), North Dakota (Fisher statistic = 5.29, df = 5, $P = 0.38$), or Wisconsin (Fisher statistic = 1.84, df = 5, $P = 0.87$).

[b] There were significant differences among total mean clutch counts (ANOVA, $F_{2,207} = 15.9$, $P < 0.0005$), brood counts/occupied nest (ANOVA, $F_{2,440} = 22.3$, $P < 0.0005$), brood counts/successful nests (ANOVA, $F_{2,359} = 12.9$, $P < 0.0005$), and total nest success ($X^2_2 = 24.11$, $P < 0.0005$). Row values for total clutch and brood counts with different superscript (D, E, F) differ between study areas (Tukey Test, all Ps < 0.0005); total nest success rates differed between BC and ND (X^2_1, = 23.78, $P < 0.0005$), BC and WI (X^2_1, = 5.61, $P = 0.02$), and ND and WI (X^2_1, = 7.54, $P = 0.007$).

[c] Occupied nest.

[d] Successful nest.

[e] Nest success.

RESULTS

We did not detect significant between-year variation for clutch size, brood size (for occupied or successful nests), or nest success within any of our three study sites. Overall differences of these reproductive attributes among study areas appear not to result from inter-year variation within study sites (Table 1).

Mean clutch size significantly differed among the three study sites over a 6-year period and was highest in British Columbia and lowest in North Dakota (Table 1). Mean clutch size significantly differed between British Columbia and North Dakota, and between North Dakota and Wisconsin, but not between British Columbia and Wisconsin (Table 1). Clutch size in North Dakota was smaller than in British Columbia in all study seasons, and smaller than clutch size in Wisconsin in all years but 1995 (when it was identical) of five study seasons (Table 1).

TABLE 2. Reproductive effort and success for Cooper's Hawks in British Columbia (BC), North Dakota (ND), and Wisconsin (WI), 1995–2001. Numbers in parentheses are percentages.

	Study area		
	BC	ND	WI
Eggs/clutch			
1	1 (1)	2 (6)	0 (0)
2	1 (1)	2 (6)	2 (2)
3	8 (11)	8 (25)	10 (10)
4	23 (31)	19 (59)	52 (50)
5	41 (55)	1 (3)	37 (36)
6	1 (1)	0 (0)	2 (2)
Total clutches	75	32	103
Young/brood			
1	10 (7)	6 (7)	5 (4)
2	16 (11)	14 (18)	13 (10)
3	27 (18)	34 (42)	26 (19)
4	63 (43)	26 (33)	61 (45)
5	31 (21)	0 (0)	31 (23)
Total broods	147	80	136

Most Cooper's Hawk clutches (55%) had five eggs in British Columbia. Many clutches (36%) in Wisconsin also had five eggs, but in North Dakota only one of 32 clutches (3%) had five eggs (Table 2). British Columbia and Wisconsin populations both exhibited a few six-egg clutches, but no clutches with >five eggs were detected in North Dakota.

Mean brood sizes at occupied (i.e., eggs laid) and successful nests (i.e., one nestling ≥18 days of age) at these three study sites across 6 study years had the same pattern as clutch sizes: significantly higher in British Columbia and Wisconsin versus North Dakota, but not significantly different in British Columbia versus Wisconsin (Table 1). North Dakota had the smallest mean brood size in both occupied and successful nests in each of six study seasons, and Wisconsin had the highest mean brood size in successful nests and British Columbia had the highest brood size in occupied nests (Table 1).

Brood size in successful nests ranged from one to five young in British Columbia and Wisconsin, and the majority of broods at each of these study sites contained four (43–45%) or five (21–23%) nestlings. Brood size at successful nests in North Dakota ranged from one to four, and most broods had three (42%) or four (33%) nestlings (Table 2). Thus, 67% of successful nests in North Dakota but only 32–36% of successful nests in Wisconsin or British Columbia had ≤3 young/brood.

Nest success also differed among study sites with British Columbia (91%) significantly higher than Wisconsin (82%) and North Dakota (68%) significantly lower than the other two sites (Table 1). Nest success rates were lower in North Dakota versus the other two sites in each of six study seasons.

DISCUSSION

Several reproductive indices—clutch size, brood size, and nest success—differed significantly among or between two or more of three northern breeding populations of Cooper's Hawk in geographically and ecologically diverse landscapes in British Columbia, North Dakota, and Wisconsin during 1995–2001. North Dakota consistently had lower reproductive indices than British Columbia and Wisconsin. Comparisons of clutch, brood size (both occupied and successful nests), and nest success between North Dakota and the other two study sites over six study seasons differed in all indices in all but one case (clutch size vs. Wisconsin in 1995; Table 1). Mean clutch size in North Dakota was 79–82% of the means for British Columbia and Wisconsin, while mean brood size for successful nests in North Dakota was 81–83% of the means for British Columbia and Wisconsin. Hatchling mortality rates were not responsible for the similar disparity in brood sizes in successful nests between North Dakota and the other two study sites.

Body mass or size of breeding adult Cooper's Hawks has been shown to be positively related to reproductive effort in Wisconsin (Rosenfield and Bielefeldt 1999). However, it does not appear that differences in body mass of nesting adults were responsible for the lower clutch and brood sizes in North Dakota, where breeding birds were not significantly different in mean mass versus males and females in British Columbia (Rosenfield 2006). Breeding birds on the two western study sites had significantly less mean body masses than Wisconsin males and females (Rosenfield 2006). Despite the disparity in body mass, Cooper's Hawks in Wisconsin do not have clutch or brood sizes significantly different from those in coastal British Columbia.

In some populations, second-year (SY), brown-plumaged breeding Cooper's Hawks that are 1 year of age are known to exhibit lower production than gray plumaged, after second year breeding birds >2 years of age (e.g., Boal 2001). We found SY birds were breeding each year in Wisconsin and British Columbia, averaging 3 and 26% of the total breeding birds in these areas, respectively (Stout et al. 2006, 2007). In contrast, we detected SY birds in only 1 year and overall they made up <1% of the total number of breeding birds in North Dakota (Rosenfield et al. 2003, Rosenfield 2006). Despite the marked disparity in proportionate number of SY birds in our study populations, Wisconsin and British Columbia do not have clutch or brood sizes significantly different from each other. The low percentage of SY birds in North Dakota could not have been responsible for the comparatively lower clutch and brood sizes found there.

Nenneman et al. (2003) suggested that Cooper's Hawks in North Dakota now exploit nesting habitat that has only recently become available; and that this species may now be the most common breeding raptor in the sparsely distributed woodlands of northwestern North Dakota. It seems unlikely that nest tree availability would depress reproductive indices in North Dakota, where nesting densities are similar to those in British Columbia and Wisconsin (Rosenfield et al. 1995, Bielefeldt et al. 1998, Rosenfield et al. 2002a, Nenneman et al. 2002).

Food availability may have influenced the reproductive indices that we documented among our study sites. Raptor populations, especially those that are more geographically peripheral to those in the center of the breeding range, can exhibit reproductive responses to changing food supplies (Newton 1979, Caughley et al. 1988, Reynolds et al. 1992, Lawton 1993, Wiens et al. 2006; but see Marti 1994). However, we were unable to detect inter-year variation in productivity within any of our study sites near the northern edge of the breeding range of the Cooper's Hawk across a relatively long period. We have also failed in other long-term studies of 16–18 years to find a relationship between reproductive effort and the presumptive quality of nest sites for Cooper's Hawks in Wisconsin (Rosenfield and Bielefeldt 1999, Rosenfield et al. 2000). It also seems unlikely that food is a limiting factor in North Dakota where breeding populations of Cooper's Hawks appear to be increasing (Nenneman et al. 2002). We do not believe that food availability *per se* is a likely explanation for the consistent variation in reproduction we found among study sites. Nesting Cooper's Hawks in our British Columbia study area are mostly sedentary (Campbell et al. 1990). The breeding population in Wisconsin is partly migratory (Rosenfield and Bielefeldt 1993, Bielefeldt et al. 1998), while nesting birds in North Dakota are highly migratory (Meehan et al. 2003). Breeding schedules of Cooper's Hawks in northwestern North Dakota are consistently about 2–3 weeks later than those of birds at comparable latitudes in British Columbia and Wisconsin (Murphy and Ensign 1996, Bielefeldt et al. 1998, Rosenfield et al. 2002a). The energetic demands of migration and the phenological constraints of a shorter breeding season might limit the ability of hawks to accumulate energetic reserves for egg production (Meiri and Yom-Tov 2004). Understanding how food availability may influence the physiology of egg production in migrant versus non-migrant Cooper's Hawks is needed to address this hypothesis (Nol et al. 1997).

We have no explanation as to why nest success rates were higher in British Columbia versus the other two sites (Table 1) because most unsuccessful nests at all three study sites failed for unknown reasons. However, nests placed closer to the ground, such as those in our North Dakota study area (Rosenfield et al. 2002a, Nenneman et al. 2003), may have greater predation risk than nests placed higher from the ground (Newton 1979, Steenhof 1987).

Data on reproductive indices, nesting densities, and nest area reoccupancy for North Dakota and for our study sites in British Columbia and Wisconsin, are consistent with populations that are at least stable and possibly increasing (e.g., Rosenfield et al 1995, Nenneman et al. 2002).

Body mass and ages of nesting hawks, hatchling survival rates, nest site availability, and breeding density do not appear to be related to the variation of reproductive indices among sites, or to the lower reproductive indices in North Dakota. However, these three populations of Cooper's Hawks differ not only in reproductive attributes, but in morphometrics, migratory behavior, nesting phenology, and landscape level habitat use. Reproductive indices may be more sensitive to environmental changes than adult survival (Wiens et al. 2006). These indices also can aid in assessing the quality of breeding habitat for Cooper's Hawks (e.g., Boal and Mannan 1998, Rosenfield et al. 2000, Rosenfield and Bielefeldt 2006, Stout et al. 2007).

It is possible that land managers could draw incorrect conclusions about the suitability of breeding habitat in North Dakota if it were assumed the comparatively lower reproductive indices, such as brood counts per occupied nests in 1995 and 1998 (Table 1), indicated productivity deficiencies. This is especially the case when biologists lack information on clutch sizes, which were linked to the comparatively smaller brood sizes there. However, the study population of Cooper's Hawks in North Dakota, where it is considered a species of special concern, appears to be viable and increasing (Nenneman et al. 2002). We believe that clutch size data in our study were crucial for assessing reproduction and encourage raptor researchers to consider the feasibility of obtaining this metric in their reproductive studies.

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HABITAT RELATIONSHIPS OF BIRDS OVERWINTERING IN A MANAGED COASTAL PRAIRIE

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ABSTRACT.—Grassland birds are considered to be rapidly declining in North America. Management approaches for grassland birds frequently rely on prescribed burning to maintain habitat in suitable condition. We evaluated the relationships among years since burn, vegetation structure, and overwintering grassland bird abundance in coastal prairie. Le Conte's Sparrows (*Ammodramus leconteii*) were most common in areas that had: (1) been burned within the previous 2 years, (2) medium density herbaceous vegetation, and (3) sparse shrub densities. Savannah Sparrows (*Passerculus sandwichensis*) were associated with areas: (1) burned within 1 year, (2) with sparse herbaceous vegetation, and (3) with sparse shrub densities. Sedge Wrens (*Cistothorus platensis*) were most common in areas that had: (1) burned greater than 2 years prior and (2) dense herbaceous vegetation. Swamp Sparrows (*Melospiza georgiana*): (1) were most common in areas of dense shrubs, (2) not related to time since burnings, and (3) demonstrated no relationship to herbaceous vegetation densities. The relationships to fire histories for all four bird species could be explained by the associated vegetation characteristics indicating the need for a mosaic of burn rotations and modest levels of woody vegetation. *Received 19 October 2005. Accepted 3 September 2006.*

Population declines of grassland birds have been more severe than for any other group of birds in North America (Peterjohn and Sauer 1999, Sauer et al. 2004). Declines have been attributed to degradation and loss of habitat in both breeding and wintering areas (Knopf 1994, Arey et al. 1998, Peterjohn and Sauer 1999). Prescribed fire is commonly used to manage habitat conditions for birds in some grassland types (Van't Hul et al. 1997, Madden et al. 1999, Tucker and Robinson 2003), particularly in the southeastern United States. The effects of different burn rotations are generally not well defined, in part, because factors not necessarily related to fire are also important for grassland bird management. For example, vegetation structure has been associated with grassland bird abundance (Wiens and Rotenberry 1981, Cully and Michaels 2000), but the responses of vegetation following fire can be influenced by factors such as rainfall, soil type, and season of burning. Since fire is a primary means of managing grasslands and grassland birds, it is imperative that we understand bird species use patterns of burned habitat and the role of habitat structure.

The coastal prairie is the southernmost unit of the tallgrass prairie biome and lies along the northwestern coast of the Gulf of Mexico. This ecosystem is listed as "imperiled globally" by The Nature Conservancy and the Texas Natural Heritage Program lists it as "critically imperiled" (Grace 2000). Coastal prairie once spread over 2.4 million ha from southwest Louisiana to the lower Texas coast (Arey et al. 1998). Less than 1% of the historic coastal prairie ecosystem now remains in relatively pristine condition (Diamond and Smeins 1984, Arey et al. 1998). Specific objectives of fire management for coastal prairie include frequent burn rotations (generally every 3–5 years), to suppress growth of woody plants, primarily eastern baccharis (*Baccharis halimifolia*) and Chinese tallow tree (*Triadica sebifera*), to maintain open grassland habitat (Grace 1998, Allain and Grace 2001).

We investigated the relative abundance of Le Conte's Sparrow (*Ammodramus leconteii*), Sedge Wrens (*Cistothorus platensis*), Savannah Sparrow (*Passerculus sandwichensis*), and Swamp Sparrow (*Melospiza georgiana*) in areas burned within the previous 1, 2 or 3 years to examine the effect of fire on herbaceous and woody vegetation, and habitat associations of individual bird species.

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METHODS

Study Area.—Our study was conducted during winter 2002–2003 at the Hoskins Mound (upland coastal prairie) portion of the Brazoria National Wildlife Refuge along the upper Texas coast of the Gulf of Mexico. Historically, the land was used for cattle and rice production, resulting in the dissection of the refuge into numerous well-defined units surrounded by fire breaks such as levees, roads, and ditches. The units studied have not been grazed or farmed since at least 1990 (J. B. Grace and L. K. Allain, pers. comm.). Dominant plant species in the units studied included little bluestem (*Schizachyrium scoparium*), broom sedge (*Andropogon virginicus*), saltmeadow cordgrass (*Spartina patens*), switchgrass (*Panicum virgatum*), cutover muhly (*Muhlenbergia capillaris* var. *trichopodes*), narrowleaf marshelder (*Iva angustifolia*), longspike tridens (*Tridens strictus*), rosette grass (*Dichanthelium* spp.), and sedges (*Cyperus* spp.). Eastern baccharis is a native and invasive shrub common in coastal areas. This species occurred in scattered clumps throughout much of the refuge and dominated portions of many units. Other woody trees and vines on study sites included blackberry (*Rubus* spp.), Macartney rose (*Rosa bracteata*), wax myrtle (*Morella cerifera*), and Chinese tallow tree.

Approximately 3,200 ha of upland prairie on the refuge are actively managed with prescribed burning. The burning program was established in 1997 with emphasis on growing season fires. Mowing and haying have also been used for management of some areas. The management plan seeks to achieve an average burn rotation of 3–5 years, depending on site conditions and successional status.

Field Methods.—We selected 15 burn units for study with five replicates for each of three burn histories (burned within the past 1, 2, or 3 years). We did not sample areas burned beyond 3 years because we did not expect Le Conte's Sparrow in sufficiently comparable numbers. Units ranged in size from 40 to 520 ha. Twelve 100-m transects were randomly located in each unit using a randomization procedure in ARC-GIS with the restriction they had to be a minimum of 50 m apart and have a 50-m buffer zone from edges such as roads and firebreaks. All transects were surveyed once for birds and vegetation. Three transects from each burn treatment were surveyed each day (n = 9, 100-m transects/day) and units were selected in random order. Thus, 180 line transects were surveyed.

Protocols for line transect surveys were designed to survey grassland birds (Shackelford et al. 2001, Carrie et al. 2002). Transect direction was northeast to southwest because birds were more easily identified when the sun was behind the observer. A team of three people, consisting of one observer and two "beaters" who disturbed vegetation with 3-m poles, walked each transect. Individual birds were identified in flight because most are difficult to observe in grasslands and usually do not perch, sing, or call in winter. We recorded species and distance from the center line in 1-m increments from where the bird was first observed. We conducted surveys when weather conditions were not expected to impede our ability to detect birds (i.e., rain, fog, or wind speed ≥20 km/hr; Gabrey et al. 1999).

Vegetation was sampled after completing bird surveys each day. Vegetation characteristics were measured at three random points within 10 m along each transect line (n = 540 points). Selection of habitat variables was based on previous studies that examined habitat associations with birds in similar environments (Pulliam and Mills 1977, Wiens and Rotenberry 1981, Skinner 1982, Thatcher et al. 2006). Height of herbaceous vegetation was measured by recording the tallest herbaceous vegetation within 1 m of each point from four cardinal directions. Herbaceous density was measured using a variation of the pole method (Plentovich et al. 1999) modified from Mills et al. (1989). We recorded the number of herbaceous contacts on a pole (~5 cm in diameter) in 5-cm increments up to 20 cm (sum of 0–20 cm increments) to measure ground density, or leaf litter. We counted the number of contacts every 10 cm up to 2 m (sum of 0–200 cm increments) to measure overall herbaceous density (VEGDEN). The maximum number of contacts counted for each increment (every 5 or 10 cm) was 10 (Plentovich et al. 1999). Community type was recorded for each transect based on the dominant plants (little bluestem, saltmeadow cordgrass, or a mixture of these two species).

Woody vegetation density, primarily composed of eastern baccharis, was measured using the point-centered quarter (PCQ) method (Cottam et al. 1953). We estimated woody plant density by measuring the distance to the nearest woody plant in each of four quadrants (northwest, northeast, southwest, southeast) at each sample point along transects. Each woody plant was placed into a size class by height (e.g., 0–1.0, 1.1–2.0, 2.1–3.0 m, etc.). Density was estimated for all woody plants (ALLSHR), live eastern baccharis (LBACC), and dead eastern baccharis (DBACC). Presence or absence of all shrub/tree species was recorded [Macartney rose, wax myrtle, Chinese tallow tree, elm (*Ulmus* spp.), and holly (*Ilex* spp.)].

Data Analyses.—Program DISTANCE was used to evaluate which detection variable might bias estimates of population densities to enhance overall density estimates of the four most common bird species (Buckland et al. 2001, 2004). It was necessary to convert the bird survey data to presence/absence (categorical) responses to analyze habitat associations. Vegetation variables were categorized into low, medium, and high categories by number of total observations.

We used structural equation modeling (SEM) (Bollen 1989, McCune and Grace 2002, Pugesek et al. 2004, Grace 2006) to examine multivariate relations between individual bird species and habitat conditions. SEM is a tool for comparing observed patterns in data to those predicted from hypothesized path models, typically relying on maximum likelihood procedures for solution. The resulting estimates for path coefficients in structural equation models represent the implied sensitivities of response variables to variations in individual predictors (Grace and Bollen 2005).

The goals of the SEM analyses were to: (1) examine the extent to which the association of birds with different post-burn conditions could be explained by related habitat features, and (2) estimate the relative sensitivities of birds to different vegetation conditions using Mplus (Muthén and Muthén 2004). We performed SEM in a categorical modeling mode because the response variable, presence or absence of bird species in a transect, is binary.

We examined the data for forms of bivariate relationships between predictor and response variables using both graphical techniques and exploratory logistic regression. The results indicated nonlinear relationships (e.g., the probability of observing a bird of a particular species was highest at some intermediate level of vegetation density) for all of the predictors. Attempts to model these results using polynomial models were inefficient (large, systematic deviations). We tried an alternative approach to modeling nonlinear relationships that involved categorizing continuous response variables and treating the categories as fixed-state dummy variables (Grace 2006). This approach to modeling nonlinear relationships was consistently more efficient.

Bivariate associations between individual predictors and bird responses were calculated for descriptive purposes. The presentation of these results was for comparisons between raw, bivariate/univariate relationships. The predictors used in the SEM analysis were all categorical (years since burn, vegetation density categories, and vegetative community types) and we used categorical modeling methods (PROC FREQ; SAS Institute, Inc. 1999) to describe associations and narrow the variables used.

Nesting of transects within burn units was accommodated in the SEM using the "cluster" option in Mplus. This option accounts for non-independencies in the data by calculating adjusted standard errors and alternative tests of model fit that are robust to hierarchical sampling (Muthén and Satorra 1995). Model fit for all analyses (one for each of the four most common bird species) was assessed using Chi-squares calculated from a negative log-likelihood fitting function. *T*-values and their associated *P*-values for individual parameters were used in interpreting results. The *alpha* level used for model evaluations was 0.05. All results presented are based on models having good measures of fit.

We included composite variables (Heise 1972, Bollen and Lennox 1991) in models when the net effect of two related and strongly intercorrelated variables was of interest. Composite variables represent the net strengths of multiple pathways in a single path, permitting the overall sensitivity of birds to a category of influences such as time since burn or vegetative community types to be represented.

TABLE 1. Percent of transects in each category of total pole contacts or herbaceous density (VEGDEN) and shrub density (SHRUBDEN) across burn treatments. Both variables vary between burn years ($P < 0.05$).

	Burn 1			Burn 2			Burn 3		
	Low	Medium	High	Low	Medium	High	Low	Medium	High
VEGDEN	76.6	16.7	6.7	20.6	42.9	36.5	5.0	30.0	65.0
SHRUBDEN	53.3	11.7	35.0	33.3	38.1	28.6	13.3	50.0	36.7

RESULTS

Little bluestem was the most common community type (dominating 44% of all sites), saltmeadow cordgrass was second (dominating 29%), while 27% of the sites were dominated by a mixture of both species. We observed 314 birds representing 18 species during transect surveys. We observed a mean of 1.1 ± 0.08 (SE) bird species per transect conducted per site per day and a mean of 5.3 ± 0.43 species per burn unit. Species richness per burn unit was not different across burn years (df = 8; 1 vs. 2, $t = -0.17$, $P = 0.87$; 1 vs. 3, $t = 0.30$, $P = 0.77$; 2 vs. 3, $t = 0.74$, $P = 0.48$). The less common Grasshopper Sparrow (*Ammodramus savannarum*) ($n = 2$), Sprague's Pipit (*Anthus spragueii*) ($n = 2$), and Sandhill Crane (*Grus canadensis*) ($n = 7$) were only observed in first year burns.

Bird Abundance.—Histograms (program DISTANCE) revealed that detection probability decreased as distance from the center line increased for all species except Savannah Sparrow. The pattern for Savannah Sparrow suggested the birds moved away from the observer prior to detection. Thus, for this species, the detection curve was adjusted using standard DISTANCE methods, permitting an estimate of abundance.

Abundance of Le Conte's Sparrows was estimated to be 4.91 ± 1.49 (SE) birds/ha with a 0.54 ± 0.13 probability of detecting all individuals within the survey area. Estimated standard half-width (ESW) was 2.17 ± 0.51 m with truncation at 4 m. Estimated abundance of Savannah Sparrows was 2.87 ± 0.90 birds/ha with a 0.78 ± 0.11 probability of detecting all individuals within the survey area. ESW was 4.66 ± 0.66 m with truncation at 6 m. Sedge Wrens had an estimated abundance of 5.55 ± 1.97 birds/ha with a 0.45 ± 0.14 probability of detecting all individuals within the survey area. Raw observations were truncated at 5 m and analyses produced an ESW of 2.27 ± 0.69 m. Estimated abundance of Swamp Sparrows was 4.40 ± 1.48 birds/ha with a 0.63 ± 0.09 probability of detecting all individuals within the survey area. ESW was 3.16 ± 0.44 m with truncation at 5 m.

Vegetation Associations with Fire.—Burn year was significantly associated with every herbaceous and shrub variable except community type. Both vegetation measures (VEGDEN, SHRUBDEN) increased from sparse to dense as time after burn increased (Table 1). Community type had no association with time since burn, consistent with *a priori* expectations.

Bird Associations with Fire.—A significant relationship was found between burn year and the occurrence of three of the four most common bird species (Fig. 1A). Le Conte's Sparrows were more common in 2- than 3-year burn sites (df = 2, $P = 0.016$), Savannah Sparrows were more common in 1- than 2- (df = 2, $P < 0.001$) and 3-year burn sites (df = 2, $P < 0.001$), and Sedge Wrens were more common in 2- (df = 2, $P = 0.015$) and 3-year burn sites (df = 2, $P < 0.001$) than in 1-year burn sites. There was no significant difference between 2- and 3-year burn sites nor were significant relationships found between burn year and the occurrence of Swamp Sparrows.

Bird Associations with Vegetation.—Le Conte's Sparrows were more commonly observed in areas of medium vegetation density (df = 2, $P = 0.015$) and sparse shrubs (df = 2, $P = 0.018$) (Fig. 1). Le Conte's Sparrows were less common where Macartney rose (df = 1, $P = 0.003$) was present, and more common where wax myrtle (df = 1, $P = 0.005$) was present. Le Conte's Sparrows were also more common in mixed versus saltmeadow cordgrass (df = 2, $P = 0.047$). Savannah Sparrows were more common in areas with sparse herbaceous density (df = 2, $P < 0.001$) and sparse shrub density (df = 2, $P < 0.001$) (Fig. 1). Savannah Sparrows were more com-

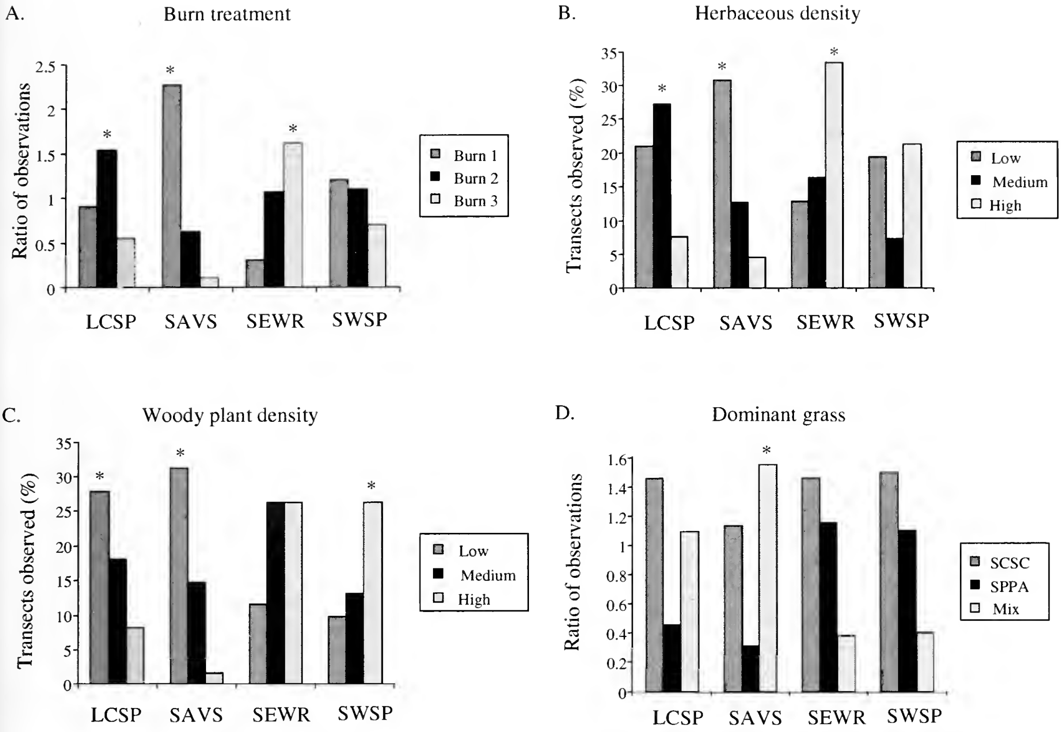

FIG. 1. Ratio (observed/expected) of observations for (A) burn treatment, and (D) community type (dominants). Percent transects birds were observed in high, medium, and low categories of (B) herbaceous density, and (C) woody plant density. Asterisks (*) indicate differences ($P < 0.05$) among categories in a category. LCSP—Le Conte's Sparrow, SAVS—Savannah Sparrow, SEWR—Sedge Wren, and SWSP—Swamp Sparrow.

monly observed in areas with high densities of eastern baccharis (df = 2, $P < 0.001$) and where Chinese tallow tree (df = 1, $P < 0.001$), Macartney rose (df = 1, $P = 0.001$), and other woody species (df = 1, $P = 0.012$), including *Ulmus* spp., *Ilex* spp., and other unidentifiable woody plants were absent. They were also more common in mixed versus little bluestem and saltmeadow cordgrass (df = 2, $P = 0.003$). Sedge Wrens were more common in areas of dense herbaceous vegetation (df = 2, $P = 0.011$) with no significant relationships to total shrub densities (Fig. 1). They were more common in areas where eastern baccharis (df = 1, $P = 0.006$) and Chinese tallow tree (df = 1, $P = 0.009$) were present. Sedge Wrens were more common in little bluestem (df = 2, $P = 0.049$) or saltmeadow cordgrass (df = 2, $P = 0.019$) compared to mixed stands (Fig. 1D). Swamp Sparrows were not associated with a particular level of vegetation density, but were more common in areas of dense shrubs (df = 2, $P = 0.035$) (Fig. 1C). They were also more common in areas where Chinese tallow tree (df = 1, $P = 0.042$) and other woody species (df = 1, $P < 0.001$) were present.

Structural Equation Model.—SEM results for Le Conte's Sparrows (Fig. 2) indicated the probability of bird occurrence was positively and directly related to a sparse density of shrubs and a medium density of herbaceous vegetation. Le Conte's Sparrows were correlated with recently burned sites (burn years 1 and 2) and this indirect relationship can be explained by the scarcity of shrubs in such sites. Le Conte's Sparrows were more likely to be in areas dominated by little bluestem or a mixture of saltmeadow cordgrass and little bluestem than in areas that were saltmeadow cordgrass. Le Conte's Sparrows (Fig. 2) were most strongly associated with open areas with sparse shrubs (shrublow) (standardized path coefficient = 0.47) and less related to medium herbaceous densities (herbmed) and the two

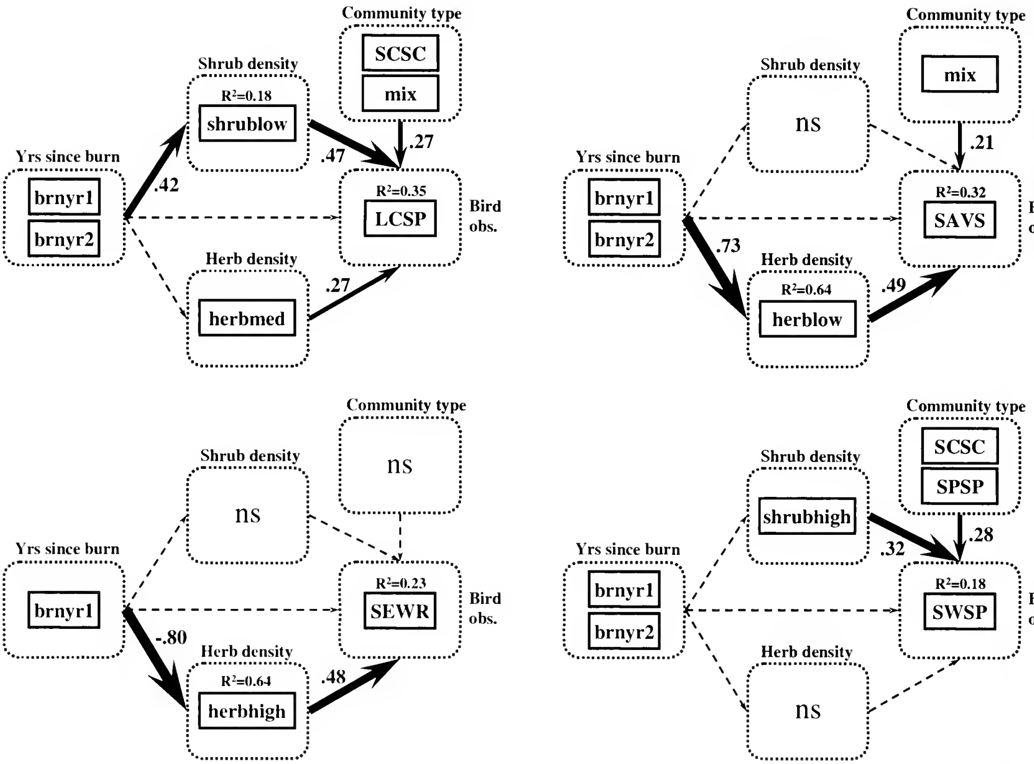

FIG. 2. Structural equation model for Le Conte's Sparrow (LCSP), Savannah Sparrow (SAVS), Sedge Wren (SEWR), and Swamp Sparrow (SWSP). Rectangles representing measured variables (e.g., brnyr1) shown inside constructs (dotted boxes) were significant contributors to prediction. Constructs that possessed no significant predictors of bird observations are labeled ns. Abbreviations represent variables; "brnyr" refers to burn year, "shrublow" refers to low densities of shrubs, "herblow" represents a low density of herbaceous vegetation, and "SCSC" represents composite effects of the *Schizachyrium scoparium* community type and "SPSP" represents *Spartina spartinae*. Parameter values presented are standardized path coefficients representing the predicted sensitivities of response variables. Dashed lines indicate paths not detectably different from zero.

community types containing little bluestem (both with coefficients of 0.27).

Savannah Sparrows were more commonly observed in areas with sparse herbaceous vegetation, regardless of shrub densities (Fig. 2). These areas were tightly associated with burns within the previous year, although this species was sometimes also in areas burned within 2 years. Savannah Sparrows were directly associated with sparse vegetation, somewhat more common in the mixed-grass communities, and only indirectly related to burning regime through associated effects on vegetation.

Sedge Wrens (Fig. 2) avoided areas having sparse and medium herbaceous density. Sparse herbaceous vegetation was most strongly associated with areas burned within the previous year. Medium levels of herbaceous vegetation occurred in areas with any burn history. The occurrence of Sedge Wrens was independent of shrub densities and types, and independent of community type, being primarily in areas with dense herbaceous vegetation where fire was absent during the previous 2 years.

The Swamp Sparrow (Fig. 2) was the only species unrelated to year since burn, either directly or indirectly. This species was associated with dense shrubs, but not with herbaceous plant density. Swamp Sparrows were uncommon where the two dominant grasses were mixed, but were positively associated with both little bluestem and saltmeadow cordgrass dominated communities. Swamp Sparrows were most weakly associated with the habitat parameters measured (R^2 = 0.18).

DISCUSSION

Fire management of coastal prairie serves many purposes, among them, the creation of conditions that provide habitat for grassland-dependent birds. What is generally not known for the coastal prairie ecosystem is the extent to which bird species discriminate among habitat conditions created by burning regimes, the role of specific vegetation conditions, and which species overlap in their habitat preferences.

Relative abundance estimates were similar among the four most common species. Detection probabilities ranged from 0.78 and 0.63 for Savannah Sparrows and Swamp Sparrows to 0.54 and 0.45 for Le Conte's Sparrows and Sedge Wrens reflecting the elusive behavior expected in the wintering areas (Lowther 1996, Herkert et al. 2001).

All species, except Sedge Wrens, were associated with community type. Le Conte's Sparrows were more common in areas dominated by little bluestem and areas with a mix of the two dominant grasses suggesting they prefer areas that are characteristic of more upland prairie. Savannah Sparrows were associated with a mix of dominant grasses, characteristic of transition zones. This phenomenon may be conducive to producing areas with sparse vegetation where one dominant grass is dying while the other is becoming established. Swamp Sparrows were associated with areas dominated by either one grass or another; this association remains unclear.

Species-specific habitat preferences are expected for an avian assemblage occupying a habitat (Pulliam and Mills 1977). These preferences are generally associated with vegetation structure. Hypotheses explaining these relationships are primarily related to food abundance (Tucker and Robinson 2003) and predator avoidance strategies (Pulliam and Mills 1977). Grzybowski (1983) consistently found that solitary grassland birds did not occur in sparse vegetation in mixed-grass prairie. Le Conte's Sparrows and Sedge Wrens in our study were usually solitary when flushed and were less common in areas with sparse herbaceous vegetation. Both are known to be relatively weak flyers (Shackleford et al. 2001) and may rely on dense cover for predator defense. Differential use of sites with medium versus high VEGDEN is unclear, but may be influenced by foraging strategies and/or dietary differences (Howell 1932, Easterla 1962, Imhof 1976).

Time-since-burn was not found to have a direct relationship with any of the species in this study but strongly influenced vegetation characteristics preferred or avoided by three of the four species. The Le Conte's Sparrow was the only species to have an indirect response to time-since-burn (associated with low shrub densities), suggesting avoidance of areas with shrubs and a preference for structural homogeneity. Sedge Wrens and Savannah Sparrows were strongly associated with herbaceous density which was greatly influenced by time-since-burn. Herbaceous density and shrub density tended to increase as time-since-burn increased. There was no relationship to shrub density for Sedge Wrens and Savannah Sparrows, suggesting herbaceous density was the primary habitat variable measured in this study to predict their occurrence.

The Swamp Sparrow was the only species not associated with burning either directly or indirectly. Swamp Sparrows are not obligate prairie birds and reportedly overwinter in a variety of habitat types, such as swamps and marshes, along lakes and reservoirs, and in coastal marshes (Mowbray 1997). The area with the highest concentration of Swamp Sparrows in this study had numerous water bounded areas within the site and serving as borders. This burn unit also had the highest concentration of shrubs and small trees.

Le Conte's Sparrow, Savannah Sparrow, and Sedge Wren were strongly associated with particular vegetation conditions and, indirectly, responded in different ways to time-since-burn. Swamp Sparrows, demonstrated a weak relationship to habitat variables, probably because of its broad association with a wide variety of habitats aside from coastal prairie. Our results and observations indicate that species included in this study are responsive to vegetation succession management using fire. The occurrence of grassland sparrows generally declined in areas with dense woody plants. Our work suggests that a mosaic of coastal prairie in 2–3 year burn rotations provides suitable habitat conditions for overwintering grassland birds.

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POST-BREEDING SEASON HABITAT USE AND MOVEMENTS OF EASTERN MEADOWLARKS IN SOUTHWESTERN WISCONSIN

MICHAEL J. GUZY[1,3,4] AND CHRISTINE A. RIBIC[2]

ABSTRACT.—We used radio telemetry to study post-breeding movements of adult female and juvenile Eastern Meadowlarks (*Sturnella magna*) in southwestern Wisconsin in 2002–2004. Twenty-one adult females were found 58% of the time in their nest field regardless of nest fate. Three adult females were not found outside of the field where their nests were located. Fifteen of 18 females that moved from the nest field at least once moved to Conservation Reserve Program fields or pasture. The average maximum distance females moved was 662 m. Once females left the nest field, 61% did not return. Twelve juveniles from different broods survived to the end of the post-breeding season. Two juveniles did not move from their nest fields during the monitoring period. Eight of 10 juveniles that moved at least once moved into Conservation Reserve Program fields, remnant prairie or pasture. The average maximum distance moved by juveniles was 526 m. Once juveniles started to leave the nest field, 67% did not return. Grassy habitats appear to be important in the post-breeding period for Eastern Meadowlarks. Management should be directed toward maintaining or enhancing the amount and quality of those habitats. *Received 10 July 2006. Accepted 21 October 2006.*

Most management of habitat to benefit grassland (and other) birds has focused on the breeding season. Current recommendations for management of grasslands emphasize delaying activities such as mowing until after the peak of nesting activity (Sample and Mossman 1997). This delay may reduce losses of nests to human disturbance but ignores the needs of fledglings and adults during the critical time from fledging of young to fall migration. The time from when a young bird fledges until breeding age is the least understood portion of the life cycle (Baker 1993) and is virtually unstudied for most species. This is a critical period when birds are learning to fly, find food, and survive on their own. Survival of young during this period may be enhanced by providing critical habitat needed for foraging, shelter, and escape from predators. Birds may require different habitats or habitat conditions depending on the time of year (Baker 1993, Anders et al. 1997, Suedkamp Wells 2005). Managers should know the habitat requirements of species in all seasons if they are going to protect existing habitat, or alter current conditions or practices for the benefit of a species.

Some telemetry work has been accomplished on movement of juvenile forest birds (e.g., Wood Thrush [*Hylocichla mustelina*]) (Anders et al. 1997) and several studies have recently examined post-breeding-season movements of individual juvenile (Yackel Adams 2001, Kershner et al. 2004b, Suedkamp Wells 2005) and adult grassland birds (Kershner et al. 2004a, Walk et al. 2004). Describing habitat use was the primary objective in only one of these studies (Suedkamp Wells 2005).

The objectives of our study were to assess habitat use and movements of adult (2002–2004) and juvenile (2003–2004) Eastern Meadowlarks (*Sturnella magna*) during the post-breeding period using radio telemetry. We chose the Eastern Meadowlark because it is a common nesting species in the study area (Guzy 2005) and is sufficiently large to carry a transmitter with a battery life to potentially last through the summer.

METHODS

Study Area.—This study was conducted in western Dane, eastern Iowa, and northern Green counties in Wisconsin bounded on the north by State Highway 18–151 from approximately Mount Horeb on the east to Ridgeway on the west. The study area was 33,413 ha in size and is referred to as the Military Ridge Prairie Heritage Area (MRPHA). The

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MRPHA is in the Driftless Area which was unglaciated during the last glacial period. The topography is a series of ridges and valleys south from Military Ridge, an east-west ridge that extends from west of Madison (near Mount Horeb) west to where the Wisconsin River flows into the Mississippi River. Historically, ridge tops were mixed-grass prairie and valleys were savanna (Curtis 1959, Cochrane and Iltis 2000).

Modern land use in southwestern and southcentral Wisconsin is primarily agricultural, with a large portion of the land in pasture, hay, and small grains with relatively few hectares of corn (*Zea mays*) and soybeans (*Glycine max*) compared to other areas of Wisconsin. The MRPHA was digitized from digital orthophotos and the land use of each polygon was field verified. Approximately 27% of the land area was in pasture and idle grass. The MRPHA has numerous prairie remnants (most privately owned, but some are owned by The Nature Conservancy and the Wisconsin Department of Natural Resources) and high enrollment in the Conservation Reserve Program (CRP) (Economic Research Service 1995). It is within the boundaries of a Conservation Reserve Enhancement Program area which provides funds for long-term and permanent conservation easements.

Trapping and Telemetry.—All birds were handled in accordance with University of Wisconsin-Madison Animal Care and Use Protocol 07-6900-A01023-1-04-01. Meadowlarks were captured while on or near the nest. Nine CRP fields (average [± SE] size = 10.2 ± 1.3 ha, range 4.8–18.2 ha), four pastures (average size = 7.6 ± 0.7 ha, range 6.0–9.5 ha), and seven remnant prairies (average size = 8.3 ± 1.4 ha, range 3.5–13.3 ha) were searched for nests during May–July 2002–2004. Nest plots were chosen based on habitat type, minimum size, condition of vegetation, and uniformity of vegetation within a patch (e.g., abrupt transitions in structure were avoided). Each nest plot was searched by dragging a rope (2002) or personnel walking in a line across the area (2002–2004). Once a nest was located, a 1.5-m diameter bow net was placed at the nest along with a remote video camera (2002–2003). A video cable and trigger cord were used so the observer/trapper could be 25 m from the nest. The video camera was used to observe when an adult returned to the nest; once an adult was present, the net was released via a cord attached to the trigger. No adults were injured due to use of bow nets. Efforts were made to minimize the possibility of adults abandoning the nest when using bow nets by only trapping at nests that were well into incubation or when there were chicks in the nest. However, two nests were abandoned because of use of the bow net in 2003. Thus, in 2004, two 12-m long mist nets were placed near each nest and birds were captured either returning to or flushing from the nest.

A Federal aluminum band with a unique number and a unique combination of three color bands were placed on the bird's legs once an adult was captured. A 1.85-g Holohil BD-2G radio transmitter (Holohil Systems Ltd., Carp, ON, Canada) was placed on birds weighing >60 g (i.e., the transmitter was at or under the 3% of body weight limit required by the Bird Banding Laboratory). The transmitter was attached using an elastic harness, modified from Rappole and Tipton (1991), around the legs; this method places the transmitter on the back over the synsacrum at or near the center of gravity. A single piece of elastic beading cord was tied into two loops with a stretched length of 50–55 mm for each loop and glued to the bottom of the transmitter with cyanoacrylate glue. This loop length held the transmitter in place without being too tight on adults and was sufficiently snug on juveniles to hold the transmitter in place until the bird reached full size. The transmitter was attached by slipping a loop over one leg and between the thigh and body. The transmitter was held in place on the bird's back with one hand (the one holding the bird) while with the other hand holding the opposite leg against the bird's body and slipping the remaining loop over the tibiotarsal-tarsometatarsal joint from the back. The loop was then moved over the foot and between the bird's body and thigh. The antenna extended past the tail and the bird would eventually preen the transmitter into the feathers so the only thing visible was the antenna.

Once juveniles were within 2–3 days of fledging, a Federal aluminum leg band (no color bands) was attached along with a radio transmitter. All birds in a nest received transmitters if they appeared healthy and were sufficiently large to carry the transmitter (i.e., ≥60 g).

The battery life for transmitters was between 9 and 11 weeks, and had a ground-level line-of-sight range of ~2 km. We started locating birds when nests failed or young fledged. The monitoring period was 11 July–6 September in 2002, 4 June to 16 September in 2003, and 3 June to 8 September in 2004. We located birds every 3 days at random times from sunrise to 1800 hrs CST. The signals were used to home in on the location of the radio. If no movements could be discerned, the observer attempted to locate the bird visually to rule out mortality or transmitter loss. Because most of the land in the study area was privately owned and permission for access could not be obtained for every field used by the meadowlarks, regardless of property ownership, locations were recorded to habitat patch and type.

Frequencies of transmitters for which contact was lost were monitored while driving roads in the study area using a scanning receiver and roof-mounted omni-directional antenna to try to relocate the signals. Frequencies were checked from a fixed-winged aircraft toward the end of the season each year to locate birds that were undetectable from the ground.

Statistical Analyses.—Distances between fields were measured in ArcView GIS (Version 3.2; Environmental Systems Research Institute 1996). The exact location of a bird in a field could not be ascertained in most cases because of access and we measured distances from the center of the nest field to the center of the field where the bird was located. Location data were assigned to the following habitat types for analysis: CRP (cool-season exotic grasses, primarily smooth brome [*Bromus inermis*]), pasture, remnant prairie, and crops (including alfalfa, strip crops, or other agricultural fields).

The post-breeding period for adults was defined as the time after they successfully fledged chicks or after a nest was lost. Only data after the end of the second nesting attempt were analyzed for two birds that renested in 2004. The post-breeding period for juveniles was after the birds left the nest. This period was divided into fledging and independence intervals with these being 1–21 days after juveniles left the nest and >21 days after the juveniles left the nest, respectively, following Kershner et al. (2004b).

Individuals that lost their radios, had faulty radios, died before the end of the season, or moved from the study area were deleted from further analysis. We only analyzed adult females as only three adult males were radiomarked. We tabulated locations for each individual by habitat and included nesting field as a separate category. We calculated the proportion of locations that occurred in the nest field for the entire post-breeding period for adults. The proportion of locations that occurred in the nest field for the fledging and independence intervals was calculated separately for juveniles.

We tested whether successfully nesting adult females tended to stay more in their nest field compared to those that were not successful. We used ANOVA to test whether these proportions differed by nesting habitat. We tested if the proportion of nest field locations was the same for the two intervals using a paired *t*-test for juveniles. We used the arcsin-square root transformation on all proportions. Tests were done in S-Plus 6.2 (Insightful Corporation 2001).

We were interested in learning if adults tended to move to the same habitat type where they had nested. Equal use of habitats was tested using a Chi-squared test. Analyses were done in StatXact (Mehta and Patel 1999). We calculated the average (± SE) distance moved from the nest field and the average maximum distance moved for all birds. We tested whether distances moved by successfully nesting adult females were the same as unsuccessfully nesting adult females using *t*-tests. Tests were done in S-Plus 6.2 (Insightful Corporation 2001).

RESULTS

Transmitter Loss and Mortality

We attached transmitters to 31 adult female Eastern Meadowlarks (13, 7, and 11 in 2002, 2003, and 2004, respectively) and 41 juveniles (16 in 2003 and 25 in 2004). Nineteen females were nesting in CRP, five in pasture, and seven in remnant prairie. Twelve of the juveniles were from nests in CRP, seven from nests in pasture, and 22 from nests in remnant prairie.

Nine females (29%) and 2 juveniles (5%) lost their transmitters. The largest number of birds losing their transmitter, eight adult females, occurred in 2002 when we were refining the attachment technique. No birds lost radios in 2003 and only one adult and two juveniles lost transmitters in 2004. Transmitter loss, rather than death, was assumed because there were no signs of depredation (e.g., no tooth or other marks on transmitter, no feathers or body parts present). We were able to confirm loss of five of six transmitters on adults (i.e., color-banded birds observed after the transmitters were recovered) but neither of the two transmitters on juveniles. No confirmed radio failures were documented.

Mortality likely occurred for one adult (3%) and 12 juveniles (29%) over the 3 years of study. The transmitter from an adult meadowlark was found on the ground among feathers. Two juveniles were found dead; one had a broken leg (the band was on the intact leg). The other 10 juvenile mortalities were inferred from recovery of the transmitter. The radios were recovered with signs of predation; predators usually pulled off the leg with the band and the transmitter and feathers were often present. Eight transmitters were recovered in grassy habitat and two transmitters were found in woods.

Movements

Adults.—Twenty-two adult females retained their transmitter to the end of the monitoring period (71%); 14 females successfully fledged their young and eight did not. Twenty-one females stayed within the study area. The one female that moved from the study area in 2002 nested unsuccessfully in pasture and was found 53 days later in a CRP field, 22 km south of the nest field.

Adult females were found 58% of the time in their nest field (SE = 0.07, $n = 21$ birds; average locations per bird = 10 [range = 5–18]). This percentage did not differ by nest success ($F = 0.65$, $df_{1,2} = 1, 19$; $P = 0.43$). Successful breeders ($n = 14$) were found 63% of the time in their nest field (SE = 0.08, 95% CI = 44–73%); unsuccessful breeders ($n = 7$) were found 49% of the time in their nest field (SE = 0.14, 95% CI = 46–80%). There appeared to be a difference in proportion of locations in the nest field by nest field type ($F = 5.58$, $df_{1,2} = 2, 18$; $P = 0.013$). However, this result was affected by two females which nested in pasture and were not located outside of their nest field. Focusing on females which nested in CRP and remnant prairies showed no difference in proportion of locations in the nest field by nest field type ($F = 2.7$, $df_{1,2} = 1, 17$; $P = 0.12$).

The majority of adult females moved outside the fields where their nests were located. Only three adult females were not found outside their nest fields; two were successful nesters in pasture and one was an unsuccessful nester in CRP. Females moved, on average, 590 ± 80 m from the nest field ($n = 18$, 95% CI = 419–759 m). The average maximum distance females were located was 662 ± 86 m ($n = 18$, 95% CI = 480–844 m). Successful and unsuccessful breeders moved the same average and maximum distances from the nest field (average distance: $t = -0.35$, df = 16, $P = 0.73$; maximum distance: $t = -0.37$, df = 16, $P = 0.72$). Once a female left the nest field, 61% (11 of 18) did not return.

Eleven of 18 females that moved at least once nested in CRP and seven nested in remnant prairie. Of the adults that nested in CRP, about one third moved primarily to other CRP fields, the rest moved to other habitats (Table 1). All adults that nested in remnant prairie moved to other habitats (Table 1). Adults that nested in CRP and in remnant prairie did not differ in types of habitats to which they moved (once they moved from the nest field) ($G = 3.4$, $P = 0.38$).

Juveniles.—Twelve juveniles from different broods survived to the end of the monitoring period and had multiple observations in the fledging and independent intervals (Table 1); juveniles were tracked an average of 53 ± 6 days (SE) post-fledging ($n = 12$). There were 8 ± 0.8 (SE) locations per bird; 4 ± 0.3 locations during the fledging interval and 4 ± 0.8 during the independent interval. These 12 juveniles stayed in the study area but two other juveniles moved from the study area. A juvenile from a nest in 2003 in a CRP field was found in a CRP field 8.8 km from the nest field. A juvenile from a nest in remnant prairie in 2004 was found in a pasture 6.6 km from the nest field.

Juveniles were twice as likely to stay in their nest field during the fledging interval

TABLE 1. Modal habitat used by Eastern Meadowlarks that stayed in the Military Ridge Prairie Heritage Area in the post-breeding season, southwestern Wisconsin, 2002–2004.

				Habitat moved to:			
Age	Nest field	Total number of birds	Remained in nest field	Conservation Reserve Program field	Remnant prairie	Pasture	Crop
Adult	Conservation Reserve Program field	12	1	4	0	4	3
	Remnant prairie	7	0	4	0	3	0
	Pasture	2	2	0	0	0	0
Juvenile	Conservation Reserve Program field	3	1	0	0	1	1
	Remnant prairie	7	1	2	1	1	2
	Pasture	2	0	1	0	1	0

(proportion of nest field locations, mean ± SE = 0.89 ± 0.08) as during the independent interval (mean ± SE = 0.41 ± 0.10) (paired t = 3.5, df = 11, P = 0.005). Two juveniles did not move from their nest fields during the monitoring period (one was from a nest in remnant prairie and the other was from a nest in a CRP field). Two of the 10 juveniles that moved at least once moved into the same habitat type in which they were hatched; the other eight moved into habitats different from their nest fields (Table 1). Average distance moved was 499 ± 103 m (n = 10, 95% CI = 266–732 m). The average maximum distance moved by juveniles that stayed in the study area was 526 ± 107 m (n = 10, 95% CI = 285–768 m). Once juveniles started to leave the nest field, 67% (8 of 12) did not return there.

DISCUSSION

Adult female meadowlarks in the MRPHA were in the field where they nested almost half of the time regardless of nest fate; most birds that moved from the nest field moved to grassy habitats. Adults that nested in prairie did not move to other prairies when they moved. However, prairie is relatively rare in the MRPHA (<1% of land use), most remnants are small (<1 ha), and other equally suitable habitats (e.g., CRP) were available closer to the nest field than another prairie remnant. Adult females moved less than a kilometer on average from the nest field regardless of the outcome of the nest attempt, and these movements were interspersed with returns to the nest field. Our results contrast with observations from Illinois (Kershner et al. 2004a) where 44% of females emigrated following nest completion; the Illinois study area comprised approximately 800 ha of managed grassland in a matrix of row crop agriculture, primarily corn and soybeans.

Distances moved by juveniles in Wisconsin were less than those observed in Illinois. The average maximum distance moved by juveniles from the nest field in the MRPHA was about 0.5 km whereas the majority of last known locations for juveniles in Illinois were 1–5 km from the nest site (Kershner et al. 2004b). Only two juveniles in the MRPHA were known to have moved from the study area.

Juveniles usually stayed in the nest field until independence in the MRPHA after which most moved from the nest field into grassy habitats. Kershner et al. (2004b) reported that over 45% of locations of juveniles were in soybeans, while most juveniles avoided corn, pasture, hay, fallow, and residential areas in Illinois. Crop fields were important for juvenile meadowlarks in Missouri (Suedkamp Wells 2005) but, in contrast to Illinois, pasture was also an important habitat. The low use of crop fields in the MRPHA may be related to landscape composition and the relatively low availability of crops. Soybeans and grass/pasture comprised 39 and 18%, respectively, of the study site in Illinois (Kershner 2001) versus 30% (all row crops and strip crops combined) and 27% (idle grass and pasture combined) for the MRPHA. Most (if not all) nest fields in the MRPHA had soybeans or strip crops (usually soybeans and/or corn with alfalfa) within 400 m; despite easy access, birds spent little time in those areas. This may indicate that foraging opportunities are superior or predation risk is lower in grass habitats than in crop fields in the MRPHA. Because of the short growing season in Wisconsin, soybean plants do not grow as tall as in more southerly locations (D. J. Undersander, pers. comm.) and may not provide adequate cover from predators.

We did not see juveniles using areas with woody cover as Suedkamp Wells (2005) did in Missouri. She suggested that use of areas with woody cover was associated with predator avoidance, particularly snakes, which were the dominant predator in that system; snake activity was observed to be lower in areas of woody vegetation than in open grasslands. Snakes, while present, did not appear to be a dominant predator in the MRPHA (Anderson 2005).

Our results do not indicate any particular management strategy is needed in the MRPHA for post-breeding or fledgling Eastern Meadowlarks other than maintaining or increasing the amount of grass on the landscape. There do not appear to be any specific habitats into which birds are moving during the post-breeding-season period before migration, nor are birds moving from the nesting field during the juvenile fledging period. Other research has found crop fields, especially soybeans, to be used frequently by meadowlarks (Kershner 2001, Kershner et al. 2004b, Suedkamp Wells 2005) but we observed Eastern Meadowlarks in crops (including hay) only rarely. Coupled with the apparent rarity of long-distance movements, this suggests that conditions in the MRPHA are at least adequate to meet the needs of post-breeding and fledgling Eastern Meadowlarks and are possibly superior to nearby areas.

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EDGE RESPONSES OF TROPICAL AND TEMPERATE BIRDS

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ABSTRACT.—Tropical birds may differ from temperate birds in their sensitivity to forest edges. We provide predictions about the proportions of tropical and temperate species that should avoid or exploit edges, and relationships between natural-history characters and edge responses. We conducted exploratory meta-analyses from 11 studies using 287 records of 220 neotropical and temperate species' responses to edges to address our predictions. A higher proportion of neotropical species were edge-avoiders compared with temperate species and a higher proportion of temperate species were edge-exploiters compared with neotropical species. Edge-avoiding responses were positively associated with being an insectivore for neotropical birds, and with being of small body mass and a latitudinal migrant for temperate birds. Temperate edge-exploiters were less likely to be insectivores and migrants than temperate birds that were not edge-exploiters. A greater proportion of neotropical birds than temperate birds may be at risk from forest fragmentation if edge-avoidance is a reasonable indicator of an inability to adapt to land-cover change. Future progress in our understanding of forest bird responses to edges is dependent upon greater standardization of methods and designing studies in the context of recent theoretical developments. *Received 27 October 2005. Accepted 30 August 2006.*

The conversion of forest to other land-cover types leads to creation of edges (Murcia 1995). Species' responses to land-cover change and edge creation in temperate forests may not be generalizable to tropical forests (Sisk and Battin 2002, Stratford and Robinson 2005). Negative edge responses may be stronger in tropical than temperate systems leading to greater effects of fragmentation in tropical compared to temperate systems (Harris and Reed 2002, Fahrig 2003). Stronger responses could manifest themselves as a greater proportion of species showing negative responses to edges in the tropics, or as relatively greater negative influences of edge on population densities of species in the tropics. Here we focus on the possibility that a greater proportion of species is negatively influenced by edges in the tropics.

A recent theoretical framework suggests that species' resource requirements are an important component in understanding why some species have positive or negative responses to edge while no responses are observed for other species (Ries and Sisk 2004). We use the term resource broadly to encompass requirements such as food and the environmental conditions that an organism is able to tolerate, including, for example, light levels and temperature. We assume that resource requirements are typically narrower for tropical forest species than for temperate forest species (Marra and Remsen 1997). We consider the implications of this assumption for the proportions of species with negative and positive responses to edges in the two regions. We also explore whether insectivory and being a latitudinal migrant are associated with edge-avoidance to examine whether some consistencies exist regarding particular natural-history characters and edge responses. Edge effects are important mechanistic explanations for the negative effects of fragmentation (e.g., Didham et al. 1998, Laurance et al. 2002) and analyses to address these issues will aid in the search for patterns regarding edge response. We used data from the literature to examine five predictions.

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A Higher Proportion of Tropical Species Should Be Edge-avoiders Compared with Temperate Species.—Humid tropical forest environments, particularly in the understory, show less seasonal variability in microclimate than many other environments (e.g., Karr 1976). Tropical forests provide some resources year-round that are not found as consistently in the temperate zone (e.g., small arthropods [Greenberg 1995], fruit and nectar [Poulsen 2002]). The species inhabiting such environments are likely to be more narrow in their resource requirements than those inhabiting temperate forest (Stratford and Robinson 2005). Temperate species experience a greater range of environmental conditions during a year than most resident species of the humid tropics because of the substantial environmental differences that exist between winter and summer in the temperate zone (Karr 1976). Temperate species are physiologically capable of tolerating conditions that lineages of tropical forest species have not encountered for many generations (Stevens 1989, Stratford and Robinson 2005). Temperate species that migrate latitudinally typically encounter and use a wider range of resources (e.g., Rodewald and Brittingham 2004) than those likely to be encountered by sedentary residents of humid tropical forests. Many microclimatic differences between edge and interior cease to exist in the winter in the temperate zone, effectively eliminating non-edge habitat (Young and Mitchell 1994). In contrast, edge-interior differences in tropical humid forests should be present year-round. Thus, we expect a larger proportion of tropical than temperate species should avoid edges because more tropical species will have a lower capacity to use/tolerate the resources available in edges, which often differ from those farther from edges (Chen et al. 1993, Fox et al. 1997, Williams-Linera et al. 1998).

A Higher Proportion of Temperate Species Should Be Edge-exploiters Compared with Tropical Species.—Báldi (1996) suggested that historically higher levels of patchiness in temperate landscapes compared with tropical landscapes have resulted in a greater proportion of species adapted to edge in temperate regions compared with tropical regions. Báldi (1996) emphasized patchiness on a regional scale but if temperate landscapes showed greater patchiness than tropical landscapes on a local scale as well, we would expect that more temperate than tropical species have adapted to use resources from different and adjacent habitats. This complementary resource distribution (e.g., nest sites in one habitat and foraging sites in another) has been suggested as an important mechanism leading to positive edge responses (Ries and Sisk 2004). This prediction is distinct in that a greater proportion of avoiders in one region compared with a second region does not necessarily lead to a greater proportion of exploiters in the second region. This is because all species do not necessarily exhibit avoidance or exploitation of edges but may not respond to edges.

Insectivores Are More Likely to Show Edge-avoiding Responses Than Non-insectivores in Both Regions.—Insectivores are often specialized in their food preferences and/or foraging techniques (Snow 1976, Rosenberg 1990, Marra and Remsen 1997), necessitating a reliance on specific substrates in particular habitats with particular environmental conditions (e.g., dead leaves in understory forest). Some groups of insects may be more abundant in forest edge than interior but many groups are less abundant, with the overall effect that edge insect communities may be significantly different from interior communities (Didham et al. 1998). We expect that insect communities of the forest edge will provide lower-quality resources than insect communities of the forest interior for insectivorous birds, given their relatively high level of specialization. Nectarivores, frugivores, and granivores use food resources that are often dispersed in space and time (Karr 1976, Stiles 1985, Levey 1988a, Stiles and Skutch 1989, Blake and Loiselle 1991), making mobility and use of environments with varying conditions more likely than for many insectivores. Omnivores are flexible in their food choices, helping to buffer them from environmental variability (Karr 1976). Thus, we expect insectivores are more likely to avoid edges. We expect this effect to be stronger in the tropics because of the greater foraging and food choice specialization demonstrated by tropical compared to temperate insectivores (Marra and Remsen 1997).

Non-insectivores are More Likely to Show Edge-exploiting Responses than Insectivores

TABLE 1. Temperate studies used in analyses were between 29° N and 44° N and tropical studies were between 2° S and 9° N.

Reference	Location	Latitude	Records (*n*)
Temperate			
Brand and George (2001)	Humboldt County, CA	41° N	14
Germaine et al. (1997)	Green Mountain NF, VT	44° N	24
King et al. (1997)	White Mountain NF, VT	44° N	5
Kroodsma (1984)	Oak Ridge, Roane, and Anderson counties, TN	36° N	17
Noss (1991)	Alachua County, FL	29° N	26
Ortega and Capen (2002)	Green Mountain NF, VT	44° N	29
Sisk (1992)	San Mateo County, CA	37° N	25
Strelke and Dickson (1980)	Nacogdoches and Cherokee counties, TX	32° N	10
Tropical			
Laurance (2004)	Amazonas State (north of Manaus), Brazil	2° S	100
Restrepo and Gómez (1998)	Ricaurte Municipality, Nariño Dep., Colombia	1° N	23
Sisk (1992)	Coto Brus, Puntarenas, Costa Rica	9° N	14

in Both Regions.—Plants favored by non-insectivores, including fruit and nectar producers, are often more common in high-light areas like gaps and edges, than in intact forest (Stiles 1975, Levey 1988b, Rodewald and Brittingham 2004). Thus, where resources are concentrated at edges, it is predicted that species that rely on these resources (i.e., frugivores and nectarivores), will exploit edges (Ries and Sisk 2004).

Latitudinal Migrants in Temperate Regions are More Likely to Show Edge-avoiding Responses Than Non-migrants.—Migrants appear to be less resistant to land-cover and climate changes than non-migrant species of temperate regions and have shown declines with habitat and climatic changes (e.g., Flather and Sauer 1996, Lemoine and Böhning-Gaese 2003). The mechanisms responsible for their susceptibility to disturbance are unclear, but Stevens (1989) and O'Connor (1992) suggested that migrants are less able to withstand environmental variability than non-migrants of temperate regions. Thus, we expect migrants will be more inclined to avoid edge than non-migrants.

We did not develop a specific prediction involving body size. Some work suggests larger birds may be more sensitive to land-cover disturbance or less likely to use edge than smaller birds (e.g., Thiollay 1995, Brand 2004). However, large species may be able to use edge habitat briefly and easily leave. The travel and time costs for a small species to enter and leave edge habitat that turns out to be unsuitable may be higher relative to energy reserves than for large species. Thus, we investigated whether body size was associated with edge response in both regions to examine if any patterns existed that could guide future work.

METHODS

We searched Biological Abstracts from 1969 through early 2005 (Biological Abstracts 1969–2005) and two reviews (Kremsater and Bunnell 1999, Sisk and Battin 2002) to select 11 studies (Table 1) that estimated either abundance or density of individual species as a function of distance from an abrupt forest edge (i.e., forest-clearcut edges, forest-field edges or forest-road edges). We excluded studies that measured nest predation, nest success, or reported only species richness or abundance of avian guilds. We also excluded studies conducted at gradual edges (e.g., forest-shrubland edges) except in one case (Noss 1991), where data from several edge types were pooled but the majority of edge types were abrupt. We initially included studies from the Paleotropics as well, but these studies were few in number and we had difficulty finding natural history information for a number of the species. These studies were excluded from the final analyses. We classified the studies into those conducted in the Neotropics (between 2° S and 10° N latitude) and those conducted in the temperate zone (between 29° and 44° N latitude). We considered temperate species to be those that spent all or part of the year at or above 29° latitude and neotropical species to be those that did not meet this criterion.

We constructed two, separate binary response variables—avoiders (avoider = 1, non-avoider = 0) and exploiters (exploiter = 1, non-exploiter = 0)—to examine edge avoidance and exploitation as distinct ecological phenomena. Each species was included in each of these two response variables because we viewed these responses as independent. If a species is not an avoider, this does not predispose it to be an exploiter. Some species could have no response to edges. Thus, for our edge-avoidance analyses, non-avoiders were any species that did not exhibit edge avoidance (e.g., both exploiters and species with no response) in each region. Non-exploiters consisted of avoiders and species with no response in each region for our edge-exploitation analyses.

We designated each species in each study as an avoider (significantly greater abundance or density away from edges), an exploiter (significantly greater abundance or density at edges), or as having no response (no increase or decrease in abundance at edges) based on the conclusions reached by the authors of each original study except in three cases (Strelke and Dickson 1980, Quintela 1985, and Sisk 1992–neotropical data). We conducted our own goodness-of-fit tests with G-statistics and Williams' corrections (Sokal and Rohlf 1995) for these studies to make designations. We excluded species' records if the expected values used for designations were less than five (Siegel and Castellan 1988).

A number of species in the temperate data set had multiple records because they were detected in more than one study. Thus, we developed three temperate data sets that differ in conservatism. The most conservative data set is the "reduced temperate data set" (n = 54 species, n = 54 records) that includes only species where all studies agreed as to the designation for that species (i.e., avoider, neutral, or no response). The "one-designation temperate data set" (n = 83 species, n = 83 records) is less conservative because we included all species and assigned only one designation to each, including those that demonstrated one type of directional response (avoid or exploit) but exhibited no response in one or more of the studies. For example, if a species was designated as an avoider by two studies but showed no response in a third study, it was considered an avoider in the one-designation temperate data set. We excluded only one species from this data set (Red-eyed Vireo, [*Vireo olivaceus*]) because it had conflicting designations (i.e., both avoid and exploit) in different studies. We created and analyzed this data set because species designated as an avoider or exploiter by at least one study showed an avoid- or exploit-response in at least some situations. Some of the multiple designations likely reflected real differences in responses (Ries and Sisk 2004), but some of the no response results may have been a result of small sample sizes. Because of the exploratory nature of these analyses, we wanted to detect potential patterns if they existed. The third data set is the "full temperate data set" (n = 83 species, n = 150 records, Appendix) which includes all species (except the Red-eyed Vireo for the same reason given above) with all their designations. This data set most accurately reflects the variability in the designations of the species across the different studies.

The neotropical data set contained only one species with conflicting designations, the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and we removed the records for this species. The neotropical data set had 137 species with 137 total records (Appendix).

We tabulated the number of species exhibiting each edge response (avoider or non-avoider, and exploiter or non-exploiter) in each region to compare proportions of avoiders/non-avoiders and exploiters/non-exploiters in the temperate and neotropical regions. We are aware of the limitations of simple tabulations (Wang and Bushman 1999, Gates 2002) but the 11 studies used a variety of distances, sampling techniques, and statistical techniques that prevented us from calculating effect sizes (Chalfoun et al. 2002). We used the reduced and one-designation temperate and neotropical data sets in contingency tables, with G-tests of significance and Williams' correction (Sokal and Rohlf 1995) for these analyses. We did not use the full data set because, for contingency table analyses, a species has to be designated as having only one response.

We classified species as primarily insectivores (insectivore = 1, other = 0) based on DeGraaf et al. (1985) for temperate species. We used information from Hilty and Brown

(1986), Stiles and Skutch (1989), Karr et al. (1990), Restrepo and Gómez (1998), del Hoyo et al. (1999), Renjifo (1999), and del Hoyo et al. (2003, 2004, 2005) to classify neotropical species. We classified temperate species by latitudinal migration patterns (neotropical migrant = 1, short-distance migrant or resident = 0) using Robbins et al. (1989) and range maps (Cornell Laboratory of Ornithology Online Bird Guide [2003]). We took body mass estimates from Dunning (1993). When separate estimates were given for males and females, we used the mean of the two values. We investigated the relationships between natural-history variables and species' responses to edges by conducting separate analyses (four analyses) for each combination of response type (avoid or exploit) and geographic region (temperate and neotropical) using the one-designation and full data sets. The reduced data set was too small to use for these analyses.

Our full data set contained many different species from the same families and multiple records of some species. The avoid/exploit response may be similar for closely related species (or for multiple records of the same species). Our data would not be truly independent if this was the case and we included random effects for both species and family in a generalized mixed linear model (GLIMMIX macro in SAS, Littell et al. 1996) to control for taxonomically clustered data (e.g., Sol et al. 2005). Similarly, the exploit/avoid responses could be correlated within studies and we included study as a random effect. Insectivory and migratory traits were included as fixed effects. This approach adjusts for possible correlations within each of the groups of repeated observations (*sensu* Sol et al. 2005). We also conducted the analyses without the random effects to allow for comparisons between results.

We were unable to test for interactions between the natural-history variables, given the sample sizes. Instead we conducted *t*-tests to examine whether body mass differed for insectivores and non-insectivores using the neotropical and one-designation temperate data sets. We also used a *t*-test to examine whether body mass differed for migrants and non-migrants using the one-designation temperate data set.

We did not use Bonferroni corrections in our analyses because of recent work indicating these corrections reduce power to unreasonable levels (Roback and Askins 2005). We considered $\alpha = 0.10$ as our significance level for all analyses because of the low power of our tabulation techniques and because of the exploratory nature of our analyses.

Species' designations and natural-history characters are available from the first author. Species and family assignments generally follow the American Ornithologists' Union (2006) and Remsen et al. (2006).

RESULTS

A higher proportion of species was classified as edge-avoiders in the neotropical data set compared with either the reduced or one-designation temperate data sets (temperate: 13%, neotropical: 50%, $G = 24.10$, $P < 0.001$, $n = 191$, df = 1; temperate: 17%, neotropical: 50%, $G = 25.08$, $P < 0.001$, $n = 220$, df = 1, respectively). Proportions of species classified as edge-exploiters were equivalent in both regions when using the reduced temperate data set (temperate: 33%, neotropical: 31%, $G = 0.13$, $P = 0.72$, $n = 191$, df = 1) while a higher proportion of species was classified as edge-exploiters for the temperate zone when using the one-designation temperate data set (temperate: 48%, neotropical: 31%, $G = 6.67$, $P = 0.01$, $n = 220$, df = 1).

Temperate avoiders and non-avoiders did not differ in diet (insectivore or not, $P = 0.29$), body mass ($P = 0.16$), or whether they were a migrant or not ($P = 0.53$) for the one-designation data set, without random effects. Results were similar when random effects were included (Table 2). Using the full temperate data set, avoiders were significantly smaller than non-avoiders, without random effects ($P = 0.10$), and more likely to be latitudinal migrants than non-avoiders, with or without random effects ($P = 0.05$ and $P = 0.05$, respectively, Table 3). Exploiters were less likely to be insectivores than non-exploiters for the one-designation temperate data set, with or without random effects ($P = 0.08$ and $P = 0.08$, respectively, Table 2). Exploiters were less likely to be migrants than non-exploiters for the full temperate data set when random effects were not included in the analyses ($P = 0.07$, Table 3).

Neotropical avoiders were more likely to be insectivores than non-avoiders, with or without random effects ($P = 0.10$ and $P = 0.02$, re-

TABLE 2. One-designation temperate data set. None of the natural-history variables differed for avoiders ($n = 14$ species) and non-avoiders ($n = 69$ species). Exploiters ($n = 40$ species) were less likely to be insectivores than non-exploiters ($n = 43$ species). P-values are from mixed models containing the natural-history variable and random effect for family.

Variable	Avoider	Non-avoider	Random effects P-value	No random effects P-value
Body mass, mean ± SE	17.9 ± 4.9	35.7 ± 5.5[a]	0.16	0.16
Insectivore, % of species	50.0	34.8	0.29	0.29
Latitudinal migrant, % of species	57.1	47.8	0.53	0.53
	Exploiter	Non-exploiter		
Body mass, mean ± SE	36.7 ± 5.8	28.8 ± 7.3[a]	0.42	0.42
Insectivore, % of species	27.5	46.5	0.08	0.08
Latitudinal migrant, % of species	42.5	55.8	0.23	0.23

[a] $n = 68$ (avoiders) and $n = 42$ (exploiters) for the body mass analysis because we omitted one extreme outlier (*Corvus corax*).

spectively, Table 4). The difference in P-values with and without random effects is due to a family effect with study having no effect. Body mass did not differ for neotropical avoiders and non-avoiders, with or without random effects ($P = 0.81$ and $P = 0.63$, respectively, Table 4). Neither diet (insectivore or not) nor body mass differed for neotropical exploiters and non-exploiters, with random effects ($P = 0.20$, $P = 0.72$, respectively, Table 4). Results were similar without random effects.

Temperate migrants had a smaller body mass than non-migrants and temperate insectivores had a smaller body mass than non-insectivores ($t = -2.88$, $P < 0.01$, $n = 82$, df $= 80$ and $t = -4.54$, $P < 0.001$, $n = 82$, df $= 80$, respectively). Neotropical insectivores also were smaller than non-insectivores ($t = -2.38$, $P < 0.01$, $n = 136$, df $= 134$).

DISCUSSION

A higher proportion of neotropical species were edge-avoiders compared with temperate species while a higher proportion of temperate compared with neotropical species showed edge-exploiting responses. These patterns may help explain the apparent higher bird species richness at edges in the temperate zone (reviewed in Kremsater and Bunnell 1999, Sisk and Battin 2002) compared to the reduced bird species richness at tropical forest edges (Lovejoy et al. 1986, Dale et al. 2000, Watson et al. 2004). These patterns also suggest that forest fragmentation and edge creation may be more detrimental to neotropical species than temperate species, if edge-avoidance indicates a species' ability to withstand land-cover changes.

Work in both temperate and neotropical re-

TABLE 3. Full temperate data set. Avoiders ($n = 22$ records) were more likely to be latitudinal migrants and had smaller body mass than non-avoiders ($n = 128$ records). Exploiters ($n = 44$ records) were less likely to be latitudinal migrants than non-exploiters ($n = 106$ records). P-values are from mixed models containing the natural-history variable and random effects for family, species nested within family, and study.

Variable	Avoider	Non-avoider	Random effects P-value	No random effects P-value
Body mass, mean ± SE	20.0 ± 3.5	33.3 ± 3.4[a]	0.17	0.10
Insectivore, % of species	40.9	35.9	0.64	0.66
Latitudinal migrant, % of species	72.7	49.20	0.05	0.05
	Exploiter	Non-exploiter		
Body mass, mean ± SE	35.5 ± 5.4	29.6 ± 3.5[a]	0.60	0.37
Insectivore, % of species	29.5	39.6	0.35	0.25
Latitudinal migrant, % of species	40.9	57.5	0.14	0.07

[a] $n = 127$ (avoiders) and $n = 106$ (exploiters) for the body mass analysis because we omitted one extreme outlier (*Corvus corax*).

TABLE 4. Tropical data set. Avoiders (n = 68 species) were more likely to be insectivores than non-insectivores. There were 69 species of non-avoiders, 42 species of exploiters, and 95 species of non-exploiters. P-values are from mixed models containing the natural-history variable and random effects for family and study.

Variable	Avoider	Non-avoider	Random effects P-value	No random effects P-value
Body mass, mean ± SE	36.8 ± 6.1[a]	32.5 ± 6.4	0.81	0.63
Insectivore, % of responses	58.8	37.7	0.10	0.02
	Exploiter	Non-exploiter		
Body mass, mean ± SE	40.0 ± 10.3	32.3 ± 4.5[a]	0.72	0.43
Insectivore, % of responses	38.1	52.6	0.20	0.12

[a] n = 67 (avoiders) and n = 94 (non-exploiters) for the body mass analysis because body mass for one species, *Sclerurus caudacutus*, was not available.

gions has shown increased food resources for birds (e.g., fruit, insects, and cones) in edge or gap habitats compared with interior forest (temperate region: Jokimäki et al. 1998, Brotons and Herrando 2003, Rodewald and Brittingham 2004; tropics: Levey 1988b, Restrepo et al. 1999). Some studies have shown increased pollination and fruit consumption at edges compared to interior (Galetti 2003, Montgomery et al. 2003). However, it is possible that temperate birds are more able to take advantage of extra food in edges than neotropical birds because they are more flexible in their resource use than neotropical birds. Rodewald and Brittingham (2004) showed positive relationships between resources available in edges and bird abundances in a temperate area while frugivore abundance was not related to fruit abundance in a neotropical study (Restrepo et al. 1999).

Other factors may help explain differences in the proportion of edge-avoiders and edge-exploiters in the two regions. If edge-to-interior differences in food resources are greater in temperate regions than the Neotropics, temperate birds may have more to gain by exploiting forest edges than neotropical birds. It is also possible that temperate birds' longer history of living in patchy landscapes (Báldi 1996) has provided selective pressure to be able to exploit edge resources. In contrast, the relatively narrow environmental conditions under which many present-day neotropical species, particularly forest species, evolved (Stevens 1989), may have diminished their ability to use habitat (edges) that results from land-cover change processes including forest fragmentation (Stratford and Robinson 2005). Finally, if temperate birds' more synchronous annual cycles cause more competition for resources during the nesting season, there may be a greater impetus for them to exploit differences that exist between edge and interior, compared with neotropical species. Data to formally address these ideas are needed.

Our finding that a higher proportion of neotropical avoiders were insectivores, compared with non-avoiders, has been indicated in other studies (Restrepo and Gómez 1998, Kremsater and Bunnell 1999, Dale et al. 2000, Beier et al. 2002, but see Watson et al. 2004). Body mass did not differ for neotropical avoiders and non-avoiders, but insectivores had a significantly smaller mass than non-insectivores. This suggests that insectivory and body size may interact so that small insectivores are particularly likely to avoid edge. The relationship between insectivory and edge-avoidance was somewhat weaker when family was included as a random effect in the analysis. This finding suggests the relationship between insectivory and edge-avoidance may be driven, at least in part, by edge-avoidance by particular families of birds (e.g., the formicariids). The mechanisms that drive these patterns need to be investigated. Neotropical insectivores may avoid edge because they tend to have narrow diets, narrow ranges of tolerable environmental conditions, and use specialized microhabitats that are not available in forest edge (Rosenberg 1990, Canaday 1996, Lindell et al. 2004). Small birds may experience higher predation risk at edges or may spend large amounts of energy if they venture into unsuitable edge habitat and then have to leave. Investigations of the types of resources used by small neotropical insectivores, and the availability of these resources in edge and interior habitats, would help resolve this question. Experimental manipulations of resources such as food and light in edge and interior habitat are also needed.

The lack of a relationship between insectivory and edge-avoidance in temperate birds suggests that insectivory is not as great a driver or indicator of edge response as it is for neotropical birds. Temperate insectivores may be less specialized than neotropical insectivores and able to use a wider range of habitat types including edge. We found that migrants are more likely to avoid edge than non-migrants in the temperate zone (similar to Flather and Sauer [1996] and Sisk and Battin [2002]), indicating they may be more susceptible as a group than temperate residents to land-cover change. Temperate migrants were also smaller than temperate non-migrants, raising the possibility of an interaction between migratory behavior, body mass, and edge-avoidance.

A lower percentage of exploiters compared with non-exploiters were insectivores for the neotropical and the two temperate data sets. However, only the one-designation temperate data set showed a significant difference. The data are suggestive, if not conclusive, that species that use resources besides insects are better able to take advantage of edge resources and/or that resources that tend to be abundant in edges, compared to interior, are more useful to non-insectivores. Previous work indicates that frugivorous species are more edge-tolerant than many insectivorous species (Restrepo and Gómez 1998, Dale et al. 2000, Beier et al. 2002), although this pattern is not always strong (Beier et al. 2002) nor consistent geographically (Watson et al. 2004).

We assessed edge avoidance and edge exploitation primarily as behavioral responses (i.e., habitat selection), driven by distributions of resources. We assume that in most cases organisms are able to select appropriate habitat and this process drives much of the variation in abundance as a function of distance to edge. However, differing predation rates on individuals in edge compared to interior, or differing nest success as a result of predation or microclimate (e.g., McCollin 1998, Flaspohler et al. 2001) may influence abundance as a function of edge through demographic processes, particularly in cases where mismatches occur between what an organism perceives to be suitable habitat and what actually is suitable habitat, (i.e., ecological traps) (Gates and Gysel 1978). These processes have received substantial attention in the temperate zone but studies to investigate these processes in the Neotropics are limited and should be a priority in the future (Bátary and Báldi 2004).

We examined food resources as a first step in documenting potential relationships between edge avoidance or exploitation and the use of particular resources while we did not examine such associations with regard to nest site resources. This was partially a result of our expectation that food resources, given they are vital to every day survival while nest sites are only critical during some seasons of the year, would be more likely to show such associations, and partially a result of the lack of data on nest sites for many neotropical species. Recent work supports the idea that food requirements, particularly being an insectivore, predispose neotropical birds to being susceptible to environmental disturbance while nest site requirements do not (Sigel et al. 2006). We suggest that future work explore such potential associations because relationships with regard to resources besides food could be more subtle or complex.

Edge effects are widely recognized (Kremsater and Bunnell 1999, Ries et al. 2004), and well documented for a range of organisms and abiotic variables (e.g., Laurance et al. 2002). We were surprised at the small number of studies that addressed density and abundance of birds as a function of distance to edge. Investigators have used a range of techniques to investigate edge effects. The three neotropical studies all involved mist netting yet the investigators used different distance intervals and/or different numbers of distance categories over which to measure edge effects. We were able to counter these differences to some extent by using a similar statistical technique (*G*-tests of goodness-of-fit) to assess whether distance to edge was associated with abundance. A number of species with multiple records were classified differently by different investigators. For example, Red-eyed Vireos were detected in six studies and classified as both avoiders and exploiters, while in some studies no response was detected. It is difficult to know which multiple designations represent meaningful biological variation among populations or study sites and which are simply a result of different sampling designs. There are indications that abiotic and vegetation edge effects vary over relatively small distances near edge, and that edge effects may penetrate several hundred meters into forest (Laurance et al. 2002). We suggest intervals of 25–50 m (based on the species under consideration) to a maximum distance into forest of at least 500 m is likely to be the most useful in documenting edge effects in species abundances. Future progress in understanding patterns and processes of edge responses is highly dependent upon greater standardization among studies with regard to distance intervals, field techniques, and statistical techniques.

We also suggest that studies compare edge effects at different times of year. All of the temperate studies, except one (Noss 1991), sampled exclusively during the nesting season. However, recent work suggests that temporal effects may help explain some of the observed variation of edge responses within species (Ries et al. 2004). Patterns may be different during winter when it could be beneficial for many species to avoid edge in temperate regions (e.g., Dolby and Grubb 1999).

Our results are drawn from studies in the New World and at one general edge type. Recent work suggests that responses to edges may vary geographically (e.g., Watson et al. 2004) and among edge types (Ries and Sisk 2004). A recent theoretical framework (Ries and Sisk 2004) emphasizes the importance of considering the relative availability of resources in adjacent patch types to be able to predict the edge-responses of particular species. Increasing the geographical range of future edge studies, standardizing methodologies, and incorporating theoretical developments into study design will increase our understanding of the influences of edges on populations and communities.

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APPENDIX. Records used in analyses to examine relationships between natural-history characters and edge-avoidance or edge-exploitation. The species represent numerous families in both the neotropical and temperate data sets.

Scientific name	Family	Study[a]	Avoid	Exploit
Neotropical data set				
Crypturellus variegatus	Tinamidae	L	0	1
Geotrygon montana	Columbidae	L	1	0
Campylopterus largipennis	Trochilidae	L	0	1
Florisuga mellivora	Trochilidae	L	1	0
Heliothryx auritus	Trochilidae	L	1	0
Phaethornis bourcieri	Trochilidae	L	0	1
Phaethornis superciliosus	Trochilidae	L	0	1
Thalurania furcata	Trochilidae	L	1	0
Aglaiocercus coelestis	Trochilidae	R	1	0
Coeligena wilsoni	Trochilidae	R	0	1
Haplophaedia lugens	Trochilidae	R	0	1
Ocreatus underwoodii	Trochilidae	R	0	1
Phaethornis syrmatophorus	Trochilidae	R	0	0
Campylopterus hemileucurus	Trochilidae	S	0	0
Phaethornis guy	Trochilidae	S	0	0
Trogon rufus	Trogonidae	L	1	0
Trogon violaceus	Trogonidae	L	1	0
Chloroceryle aenea	Alcedinidae	L	1	0
Momotus momota	Momotidae	L	1	0
Galbula albirostris	Galbulidae	L	0	1
Jacamerops aureus	Galbulidae	L	0	1
Bucco capensis	Bucconidae	L	0	1
Bucco tamatia	Bucconidae	L	0	1
Malacoptila fusca	Bucconidae	L	1	0
Monasa atra	Bucconidae	L	1	0
Nonnula rubecula	Bucconidae	L	1	0
Ramphastos vitellinus	Ramphastidae	L	1	0
Campephilus rubricollis	Picidae	L	0	1
Celeus elegans	Picidae	L	0	1
Veniliornis cassini	Picidae	L	0	1
Automolus infuscatus	Furnariidae	L	1	0
Automolus ochrolaemus	Furnariidae	L	1	0
Automolus rubiginosus	Furnariidae	L	1	0
Philydor erythrocercum	Furnariidae	L	1	0
Sclerurus caudacutus	Furnariidae	L	1	0
Sclerurus mexicanus	Furnariidae	L	1	0
Sclerurus rufigularis	Furnariidae	L	1	0
Synallaxis rutilans	Furnariidae	L	0	1
Xenops minutus	Furnariidae	L	0	1
Campylorhamphus procurvoides	Furnariidae	L	0	0
Deconychura longicauda	Furnariidae	L	1	0

APPENDIX. Continued.

Scientific name	Family	Study[a]	Avoid	Exploit
Deconychura stictolaema	Furnariidae	L	1	0
Dendrocincla fuliginosa	Furnariidae	L	0	1
Dendrocincla merula	Furnariidae	L	1	0
Dendrocolaptes certhia	Furnariidae	L	0	1
Hylexetastes perrotii	Furnariidae	L	0	1
Sittasomus griseicapillus	Furnariidae	L	0	1
Xiphorhynchus pardalotus	Furnariidae	L	0	1
Premnoplex brunnescens	Furnariidae	R	1	0
Premnornis guttuligera	Furnariidae	R	0	0
Syndactyla subalaris	Furnariidae	R	0	0
Dendrocincla homochroa	Furnariidae	S	0	0
Xiphorhynchus erythropygius	Furnariidae	S	0	0
Cercomacra tyrannina	Thamnophilidae	L	1	0
Cymbilaimus lineatus	Thamnophilidae	L	0	1
Frederickena viridis	Thamnophilidae	L	1	0
Gymnopithys rufigula	Thamnophilidae	L	1	0
Hylophylax naevius	Thamnophilidae	L	0	1
Hylophylax poecilinotus	Thamnophilidae	L	1	0
Hypocnemis cantator	Thamnophilidae	L	0	1
Myrmeciza ferruginea	Thamnophilidae	L	1	0
Myrmornis torquata	Thamnophilidae	L	1	0
Myrmotherula axillaris	Thamnophilidae	L	0	1
Myrmotherula guttata	Thamnophilidae	L	1	0
Myrmotherula gutturalis	Thamnophilidae	L	1	0
Myrmotherula longipennis	Thamnophilidae	L	1	0
Myrmotherula menetriesii	Thamnophilidae	L	1	0
Percnostola rufifrons	Thamnophilidae	L	0	1
Pithys albifrons	Thamnophilidae	L	1	0
Thamnomanes ardesiacus	Thamnophilidae	L	1	0
Thamnomanes caesius	Thamnophilidae	L	1	0
Thamnophilus murinus	Thamnophilidae	L	0	1
Dysithamnus mentalis	Thamnophilidae	S	0	0
Gymnopithys leucaspis	Thamnophilidae	S	1	0
Myrmotherula schisticolor	Thamnophilidae	S	1	0
Formicarius analis	Formicariidae	L	1	0
Formicarius colma	Formicariidae	L	1	0
Grallaria varia	Formicariidae	L	1	0
Hylopezus macularius	Formicariidae	L	1	0
Myrmothera campanisona	Formicariidae	L	1	0
Grallaricula flavirostris	Formicariidae	R	0	0
Conopophaga aurita	Conophagidae	L	1	0
Attila spadiceus	Tyrannidae	L	0	1
Corythopis torquatus	Tyrannidae	L	1	0
Hemitriccus zosterops	Tyrannidae	L	0	1
Myiobius barbatus	Tyrannidae	L	1	0
Onychorhynchus coronatus	Tyrannidae	L	1	0
Platyrinchus coronatus	Tyrannidae	L	1	0
Platyrinchus platyrhynchos	Tyrannidae	L	1	0
Platyrinchus saturatus	Tyrannidae	L	1	0
Rhynchocyclus olivaceus	Tyrannidae	L	1	0
Rhytipterna simplex	Tyrannidae	L	1	0
Terenotriccus erythrurus	Tyrannidae	L	0	1
Tolmomyias assimilis	Tyrannidae	L	1	0
Mionectes striaticollis	Tyrannidae	R	0	0
Myiophobus flavicans	Tyrannidae	R	0	0
Myiotriccus ornatus	Tyrannidae	R	1	0
Pseudotriccus pelzelni	Tyrannidae	R	1	0
Mionectes olivaceus	Tyrannidae	S	0	0
Platyrinchus mystaceus	Tyrannidae	S	1	0
Snowornis cryptolophus	Cotingidae	R	1	0
Pipreola riefferii	Cotingidae	R	0	0
Phoenicircus carniflex	Cotingidae	L	1	0
Corapipo gutturalis	Pipridae	L	0	1

APPENDIX. Continued.

Scientific name	Family	Study[a]	Avoid	Exploit
Lepidothrix serena	Pipridae	L	0	1
Pipra erythrocephala	Pipridae	L	0	1
Pipra pipra	Pipridae	L	0	1
Machaeropterus deliciosus	Pipridae	R	0	0
Masius chrysopterus	Pipridae	R	0	0
Corapipo altera	Pipridae	S	0	0
Schiffornis turdina	Tityridae	L	1	0
Laniocera hypopyrra	Tityridae	L	0	1
Pachyramphus marginatus	Tityridae	L	1	0
Hylophilus ochraceiceps	Vireonidae	L	1	0
Cyphorhinus arada	Troglodytidae	L	1	0
Microcerculus bambla	Troglodytidae	L	0	1
Thryothorus coraya	Troglodytidae	L	0	1
Troglodytes aedon	Troglodytidae	L	0	1
Henicorhina leucophrys	Troglodytidae	R	0	0
Henicorhina leucosticta	Troglodytidae	S	0	0
Microbates collaris	Polioptilidae	L	1	0
Catharus fuscescens	Turdidae	L	1	0
Turdus albicollis	Turdidae	L	1	0
Myadestes ralloides	Turdidae	R	0	0
Catharus ustulatus	Turdidae	S	0	0
Myadestes melanops	Turdidae	S	0	0
Basileuterus tristriatus	Parulidae	R	0	0
Oporornis formosus	Parulidae	S	0	0
Lanio fulvus	Thraupidae	L	0	1
Tachyphonus cristatus	Thraupidae	L	0	0
Tachyphonus surinamus	Thraupidae	L	0	1
Chlorospingus semifuscus	Thraupidae	R	0	1
Arremon taciturnis	Emberizidae	L	1	0
Buarremon brunneinucha	Emberizidae	R	1	0
Cyanocompsa cyanoides	Cardinalidae	L	0	0
Saltator grossus	Cardinalidae	L	0	1
Euphonia xanthogaster	Fringillidae	R	0	0
Temperate data set				
Callipepla californica	Odontophoridae	S	0	1
Zenaida macroura	Columbidae	S	0	0
Coccyzus americanus	Cuculidae	K	0	0
Coccyzus americanus	Cuculidae	St	0	0
Coccyzus americanus	Cuculidae	N	0	1
Calypte anna	Trochilidae	S	0	0
Archilochus colubris	Trochilidae	G	0	0
Picoides pubescens	Picidae	K	0	0
Picoides pubescens	Picidae	N	0	0
Picoides villosus	Picidae	K	0	0
Picoides villosus	Picidae	O	0	0
Colaptes auratus	Picidae	S	0	1
Colaptes auratus	Picidae	N	0	0
Picoides nuttallii	Picidae	S	0	1
Dryocopus pileatus	Picidae	N	0	0
Melanerpes carolinus	Picidae	K	0	0
Melanerpes carolinus	Picidae	N	0	1
Sphyrapicus varius	Picidae	G	0	0
Sphyrapicus varius	Picidae	N	0	0
Sphyrapicus varius	Picidae	O	0	0
Empidonax virescens	Tyrannidae	K	1	0
Empidonax virescens	Tyrannidae	N	1	0
Myiarchus cinerascens	Tyrannidae	S	0	1
Sayornis phoebe	Tyrannidae	N	0	0
Contopus virens	Tyrannidae	St	0	1
Myiarchus crinitus	Tyrannidae	St	0	1
Myiarchus crinitus	Tyrannidae	N	0	0
Empidonax minimus	Tyrannidae	G	0	0

APPENDIX. Continued.

Scientific name	Family	Study[a]	Avoid	Exploit
Empidonax minimus	Tyrannidae	O	0	1
Empidonax difficilis	Tyrannidae	B	1	0
Contopus sordidulus	Tyrannidae	S	0	0
Vireo solitarius	Vireonidae	G	1	0
Vireo solitarius	Vireonidae	O	0	0
Vireo huttoni	Vireonidae	S	0	0
Vireo griseus	Vireonidae	N	0	1
Vireo flavifrons	Vireonidae	N	0	0
Cyanocitta cristata	Corvidae	K	0	0
Cyanocitta cristata	Corvidae	St	0	0
Cyanocitta cristata	Corvidae	O	0	0
Corvus corax	Corvidae	B	0	0
Aphelocoma californica	Corvidae	S	0	1
Cyanocitta stelleri	Corvidae	B	0	1
Tachycineta thalassina	Hirundinidae	S	0	1
Poecile atricapillus	Paridae	G	0	0
Poecile atricapillus	Paridae	O	0	0
Poecile carolinensis	Paridae	K	0	0
Poecile carolinensis	Paridae	St	0	1
Poecile carolinensis	Paridae	N	0	1
Poecile rufescens	Paridae	B	0	0
Poecile rufescens	Paridae	S	0	0
Baeolophus inornatus	Paridae	S	1	0
Baeolophus bicolor	Paridae	K	0	0
Baeolophus bicolor	Paridae	St	0	0
Baeolophus bicolor	Paridae	N	0	1
Psaltriparus minimus	Aegithalidae	S	0	1
Sitta canadensis	Sittidae	B	1	0
Sitta canadensis	Sittidae	O	0	0
Sitta carolinensis	Sittidae	S	0	1
Sitta carolinensis	Sittidae	K	0	0
Sitta carolinensis	Sittidae	O	0	0
Certhia americana	Certhiidae	B	1	0
Certhia americana	Certhiidae	G	0	0
Certhia americana	Certhiidae	O	0	0
Thryomanes bewickii	Troglodytidae	S	0	0
Thryothorus ludovicianus	Troglodytidae	N	0	1
Troglodytes troglodytes	Troglodytidae	B	1	0
Troglodytes troglodytes	Troglodytidae	G	0	0
Troglodytes troglodytes	Troglodytidae	O	1	0
Regulus satrapa	Regulidae	B	0	0
Regulus satrapa	Regulidae	O	0	0
Regulus calendula	Regulidae	N	0	1
Polioptila caerulea	Sylviidae	S	0	0
Polioptila caerulea	Sylviidae	K	0	0
Turdus migratorius	Turdidae	B	0	0
Turdus migratorius	Turdidae	G	0	0
Turdus migratorius	Turdidae	N	0	0
Turdus migratorius	Turdidae	O	0	1
Catharus guttatus	Turdidae	G	1	0
Catharus guttatus	Turdidae	N	0	0
Catharus guttatus	Turdidae	Ki	1	0
Catharus guttatus	Turdidae	O	1	0
Catharus ustulatus	Turdidae	B	0	1
Catharus ustulatus	Turdidae	O	0	0
Ixoreus naevius	Turdidae	B	1	0
Catharus fuscescens	Turdidae	G	0	0
Catharus fuscescens	Turdidae	O	0	0
Sialia mexicana	Turdidae	S	0	0
Hylocichla mustelina	Turdidae	G	0	1
Hylocichla mustelina	Turdidae	K	0	0
Hylocichla mustelina	Turdidae	N	1	0

APPENDIX. Continued.

Scientific name	Family	Study[a]	Avoid	Exploit
Chamaea fasciata	Timaliidae	S	0	1
Chamaea fasciata	Timaliidae	B	0	0
Dumetella carolinensis	Mimidae	N	0	1
Mimus polyglottos	Mimidae	S	0	1
Bombycilla cedrorum	Bombycillidae	O	0	1
Setophaga ruticilla	Parulidae	G	0	0
Setophaga ruticilla	Parulidae	O	0	1
Mniotilta varia	Parulidae	G	0	0
Mniotilta varia	Parulidae	St	0	0
Mniotilta varia	Parulidae	N	0	0
Mniotilta varia	Parulidae	O	0	1
Dendroica fusca	Parulidae	G	0	0
Dendroica fusca	Parulidae	O	0	0
Dendroica caerulescens	Parulidae	G	0	1
Dendroica caerulescens	Parulidae	Ki	0	1
Dendroica caerulescens	Parulidae	O	0	0
Dendroica virens	Parulidae	G	1	0
Dendroica virens	Parulidae	Ki	0	0
Dendroica virens	Parulidae	O	1	0
Wilsonia canadensis	Parulidae	O	0	0
Dendroica pensylvanica	Parulidae	G	0	0
Dendroica pensylvanica	Parulidae	O	0	1
Geothlypis trichas	Parulidae	G	0	0
Geothlypis trichas	Parulidae	O	0	0
Dendroica occidentalis	Parulidae	B	1	0
Wilsonia citrina	Parulidae	N	1	0
Oporornis formosus	Parulidae	K	0	0
Oporornis philadelphia	Parulidae	G	0	0
Parula americana	Parulidae	N	0	1
Vermivora celata	Parulidae	S	1	0
Seiurus aurocapilla	Parulidae	G	1	0
Seiurus aurocapilla	Parulidae	K	1	0
Seiurus aurocapilla	Parulidae	N	0	0
Seiurus aurocapilla	Parulidae	Ki	0	0
Seiurus aurocapilla	Parulidae	O	1	0
Dendroica pinus	Parulidae	St	0	0
Dendroica pinus	Parulidae	N	0	1
Wilsonia pusilla	Parulidae	B	0	0
Dendroica coronata	Parulidae	O	0	0
Piranga olivacea	Thraupidae	G	0	0
Piranga olivacea	Thraupidae	K	0	0
Piranga rubra	Thraupidae	Ki	0	0
Piranga olivacea	Thraupidae	O	0	0
Piranga rubra	Thraupidae	K	0	1
Piranga rubra	Thraupidae	St	0	0
Piranga rubra	Thraupidae	N	0	1
Pipilo crissalis	Emberizidae	S	0	1
Junco hyemalis	Emberizidae	S	0	1
Junco hyemalis	Emberizidae	G	0	0
Junco hyemalis	Emberizidae	O	0	1
Pipilo erythrophthalmus	Emberizidae	S	0	0
Pipilo erythrophthalmus	Emberizidae	K	0	1
Zonotrichia albicollis	Emberizidae	G	0	1
Cardinalis cardinalis	Cardinalidae	K	0	1
Cardinalis cardinalis	Cardinalidae	St	0	0
Cardinalis cardinalis	Cardinalidae	N	0	1
Pheucticus ludovicianus	Cardinalidae	G	0	0
Pheucticus ludovicianus	Cardinalidae	O	0	0
Carduelis psaltria	Fringillidae	S	0	0
Carpodacus purpureus	Fringillidae	S	0	1

[a] B = Brand and George (2001), G = Germaine et al. (1997), K = Kroodsma (1984), Ki = King et al. (1997), L = Laurance (2004), N = Noss (1991), O = Ortega and Capen (2002), R = Restrepo and Gómez (1998), S = Sisk (1992), St = Strelke and Dickson (1980).

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NESTING BIOLOGY OF THE BANDED GROUND-CUCKOO (*NEOMORPHUS RADIOLOSUS*)

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ANDREW COOK,[4] AND JORGE OLIVO[3]

ABSTRACT.—The Banded Ground-cuckoo (*Neomorphus radiolosus*) is a rare and endangered bird species whose basic biology is poorly known. We provide the first information on nesting biology for the species. We documented two nesting attempts in the Mache-Chindul Ecological Reserve, Esmeraldas Province, northwest Ecuador. Both the first nest, active in March and April 2005, and the second nest, active in May 2005, were in primary rain forest. Both nests were ~5 m above ground in small understory trees (Melastomataceae). A pair of adult Banded Ground-cuckoos attended the first nest and contributed equally to incubation, brooding, and provisioning of a single nestling. The nestling spent 20 days in the nest from hatching to fledging and was fed a wide range of both invertebrates (primarily grasshoppers) and vertebrates (mainly small frogs). The chick fledged successfully. The second nest, also attended by a pair of adults, failed during incubation. We relate our findings to what is known of other ground-cuckoo species and discuss the conservation implications of our results. *Received 23 February 2006. Accepted 3 September 2006.*

Neomorphus ground-cuckoos are relatively large, terrestrial forest birds with large crests, long tails, and iridescent plumage (del Hoyo et al. 1997). The genus includes five species, four of which occur in the Amazon Basin, although one ranges through Central America into Nicaragua (Dickinson 2003). The fifth species, the Banded Ground-cuckoo (*Neomorphus radiolosus*, Cuculidae), is endemic to the Chocó Biogeographical Region, which encompasses 100,000 km² of humid rain forest extending from the Pacific coast up the western slope of the Andes in southwestern Panama, western Colombia, and northwestern Ecuador. The region is noted for extremely high levels of diversity and endemism. For example, the Chocó supports 62 endemic bird species, the most of any mainland region in South America (Stattersfield et al. 1998, BirdLife International 2003). The Chocó also contains an outstanding diversity of plants, insects, and terrestrial vertebrates (Dodson and Gentry 1991, Dinerstein et al. 1995, Conservation International 2001). In Ecuador, <4% of the original Chocó forests remain (Sierra 1999), the other 96% having been deforested for timber, agriculture, and settlement by colonists (Conservation International 2001).

The Banded Ground-cuckoo is one of many Chocó endemics whose populations are thought to be in decline due to habitat degradation (BirdLife International 2000, 2004; Ridgely and Greenfield 2001; Greenfield 2002; Renjifo et al. 2002). It is considered "vulnerable to extinction" within Ecuador and throughout its range (Greenfield 2002, BirdLife International 2004), which is limited to northwestern Ecuador and western Colombia. The Banded Ground-cuckoo's precarious status is widely attributed to the loss of primary Chocó forests. However, a lack of information has hindered efforts to assess the species' conservation status and requirements (BirdLife International 2000, 2004; Greenfield 2002).

The Banded Ground-cuckoo is one of the rarest and least known birds in Ecuador (BirdLife International 2000, 2004; Greenfield 2002). In recent years, it has been reported from only two localities in northwestern Esmeraldas Province: in 1992 at Alto Tambo and approximately four times since 1996 from Bilsa Biological Station (Hornbuckle 1997, Hornbuckle et al. 1997, Lopez-Lanus et al. 1999, Ridgely and Greenfield 2001). Single individuals, pairs, and small family groups have been seen. Little is known of the species' basic biology or conservation requirements.

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We present the first published report on nesting biology of the Banded Ground-cuckoo, including information on parental care, and discuss the conservation implications of our findings.

METHODS

We conducted our study at the Bilsa Biological Station (79° 45′ W, 0° 22′ N, 330–730 m elevation). Bilsa is a 3,500 ha private reserve owned and operated by Fundación Jatun Sacha within the Mache-Chindul Ecological Reserve in Esmeraldas Province, Ecuador. Bilsa contains a complex mosaic of undisturbed, selectively logged, and regenerating forests that vary in size, isolation, and disturbance. The majority of Bilsa is primary forest but much of the habitat in the surrounding Mache-Chindul Reserve has been degraded. The areas surrounding Bilsa are largely deforested and used for agriculture or pasture; only isolated patches of primary and regenerating forest remain.

We trapped an adult Banded Ground-cuckoo (unknown gender) in a mist net on 4 December 2004 and applied three colored leg bands and a lightweight radio as part of a larger study of the species. The radio transmitter (model RI-2C; Holohil Systems, Carp, ON, Canada) was attached to the bird using a backpack style harness made of rubber ligature (Vehrencamp and Halpenny 1981). The 6.0-g radio weighed 1.4% of the bird's total body mass (433 g). We tracked the individual using a Telonics TR4 receiver and a RA-2AK "H" antenna until the bird led us to an active nest in March 2005. We suspended radio tracking while the nest was active to minimize disturbance. However, we used the tracking equipment to identify which bird was attending the nest if color bands were not visible, and to obtain qualitative information on movements during the incubation stage.

The radio-equipped bird and at least one other adult without color bands or radio attended the nest. We observed only one unbanded bird plus the radio-equipped individual at the nest at any one time. We believe that only two adults (presumably the male and female) attended this first nest. We used a blind 20 m from the nest to observe the birds using 10× binoculars. We also recorded, and subsequently analyzed, activity using a Sony Hi-8 digital video camera, 6 m from the nest. The birds seemed aware of us but did not appear agitated or nervous. We doubt that our presence strongly affected their behavior. We recorded identity of each adult that visited the nest, arrival and departure times, activity while at the nest, and the type of food fed to the nestling. Additionally, we collected data on egg size and coloration, development of chick plumage and behavior, habitat surrounding the nest site, nest architecture, and post-fledging behavior.

The radio-equipped bird led us to a second nest in April 2005 where it was joined by an unbanded individual. We are uncertain if the unbanded bird was the same individual that participated in the first nesting attempt. We mist netted the unbanded adult on 4 May 2005, 30 m from the second nest and attached a 6.0-g Holohil RI-2C radio transmitter (1.6% of the bird's body mass of 365 g) with a backpack style harness (Vehrencamp and Halpenny 1981). Total processing time was 38 min. We used radio-tracking equipment and visual observation to confirm this bird resumed normal incubation behavior on the afternoon of the day it was captured.

We recorded the location of the nests using hand-held Garmin GPS units. No fine-scale satellite imagery is available for Bilsa and no fine-scale maps of habitat types exist for the area. We quantified habitat characteristics within a circular plot of 20-m radius around the nest site. We estimated canopy height and counted the number of trees with a diameter at breast height (dbh) >50 cm and the number of trees in the genus *Cecropia* (Cecropiaceae) within the circular plots. *Cecropia* is a pioneer tree in Bilsa commonly found in disturbed areas, and we used it as an index of previous habitat disturbance. The trees in which the nests were placed and the plants whose leaves were used in the nests were identified by Carlos Cerón Martínez at the Herbario Alfredo Paredes, Universidad Central del Ecuador and by Lorena Carrillo at the Herbario Nacional del Ecuador.

We recorded data for 47 hrs at nest #1 during the incubation stage from 1 through 6 days prior to hatching ($n = 6$ sessions with an average of 8.0 ± 3.8 hrs per session, range = 3.0–11.5 hrs/session). We recorded data for 113 hrs during the nestling stage of nest #1 with at least one observation period on all but 3 days (n = 17 sessions, average observation period = 4.7 ± 2.2 hrs, range = 2.1–9.5 hrs/session). Data from live observations and video recordings were combined for statistical analyses and are presented as means ± SE. Feeding, brooding, and incubation rates for each of the two adults were not normally distributed (Kolmogorov-Smirnov tests, $P < 0.05$). Thus, we used non-parametric, Mann-Whitney U-tests for pairwise comparisons of parental care by the two adults. All tests were two-tailed and used a significance level of $P = 0.05$ unless otherwise stated. All analyses were conducted using SAS V.8 statistical software.

RESULTS

Nest Site Descriptions.—We documented two Banded Ground-cuckoo nests. Both nests were found by Don Jorge Olivo, the first on 2 March 2005. Nest #1 was ~60 m (elevation) and 120 m (horizontal distance) from a small river on the flank of a large hill that reached ~120 m (elevation) and 600 m (horizontal distance) from the river. The UTM coordinates of the nest were 17N 0643173, 0037755 and the elevation was 540 m.

Nest #1 was in primary Chocó rain forest. It was ~200 m from secondary forest, 600 m from the Bilsa field station, and 250 m from a major walking trail which forms the boundary of the reserve. The nest was 12 m from a trail used once per week by Bilsa volunteers and staff, and occasionally by poachers and their dogs. Chocó rain forest is extremely humid (>3 m of rainfall/year), and the forest surrounding the nest was characterized by an open understory, a closed canopy 25–30 m high, and average visibility of ~20 m. Common trees included *Otoba gordonifolia* (Myristicaceae) and *Gustavia dodsonii* (Lecythidaceae); no *Cecropia* were present. Data from the circular plot surrounding the nest indicated that canopy height was 25 m, and six trees had a dbh >50 cm. These measures are consistent with our data from 100 independent primary forest sites within Bilsa (JK, unpubl. data).

The second nest, discovered on 27 April 2005, was ~150 m south of the first nest on the same hillside (UTM coordinates: 17N 0643622, 0037809; elevation 581 m). It was in primary forest and >100 m from the nearest trail. Data from the circular plot indicated a canopy height of 28 m, two trees with dbh >50 cm, and no *Cecropia*.

Description of the Nests.—Both nests were in the same species of understory tree, *Miconia* sp. (Melastomataceae). Nest #1 was 5.4 m above ground in a 9-m tall tree with a dbh of 7.2 cm. Nest #2 was 3.9 m above ground in a 7.5-m tall tree with a dbh of 6.3 cm. Each nest was positioned close to the trunk in a large crotch formed where one or more branches radiated from the trunk. Nest #1 was built on a 5-cm diameter branch where it left the trunk; Nest #2 was built where two branches of 4 and 5 cm diameter left the trunk. The trunk of the tree with nest #1 was inclined at an angle of 60° from the ground; the adults ran up and down the trunk to access or leave the nest. The trunk of the tree with nest #2 was nearly vertical and to ascend the birds hopped up the lower branches, in effect using them as a ladder. To descend from nest #2, the birds took a few steps from the nest along the branch and glided to the ground.

Both nests were large, open cups of similar shape and size. Nest #1 measured 37 × 25 (length/width) × 13 cm high on the outside, and nest #2 measured 38 × 24 × 15 cm. Both were bulky structures with walls ~6 cm thick. The nests appeared to be made entirely of leaves. We did not see any sticks or moss supporting or anchoring the structure, or lining the inside. We recorded leaves of six species in the nests, the majority of which were from a fern (*Diplazium* sp., Aspleniaceae). Two small bromeliads, one palm, and one unknown species germinated on the wide rim while nest #1 was active and were allowed to grow. We did not record which species germinated on nest #2. Throughout the first nesting effort, the adults brought an average of two new leaves each day (usually *Diplazium* sp.) to build up the lining of the nest, but were not observed removing leaves from the nest.

Incubation Stage and Fate of the Second Nest.—Both nests were discovered in the incubation stage with a single egg. It is possible that both nests had one or more eggs removed by a predator before we found them. However, we consider it more likely the original clutch size for both nests was a single egg. Nest #1 was discovered 13 days prior to hatching; nest

#2 failed during incubation. Both eggs were uniformly cream colored but gradually acquired small brown spots as incubation progressed. The eggs were round rather than oval, with an estimated size of 4.5 × 4.0 × 4.0 cm, based on visual observation.

The two adults tending nest #1 shared incubation duties equally. The radio-equipped bird incubated an average of 3.2 ± 1.9 hrs per observation session, whereas the other bird incubated an average of 3.8 ± 2.5 hrs per observation period. Each adult was observed to remain on the nest until dark (1800 hrs) at least once (three times for the radio-equipped bird and one time for the unbanded bird), suggesting either bird incubated during the night. The egg occasionally went without incubation (max = 3 hrs), but in most cases the birds replaced each other immediately so the egg was uncovered for <30 sec. We did not take detailed data on incubation from the second nest, but we confirmed via radio-tracking that both birds incubated in approximately equal proportions. Qualitative radio-tracking data on movement by the adults indicated the birds traveled >400 m from the nest between incubation bouts (JK, unpubl. data).

The birds on the nest appeared alert but not nervous. We detected no vocalizations or interaction between the adults when they replaced each other on the nest. The birds moved the egg with their bills an average of once per 120 min during observation periods, appearing to change the part of the egg in contact with their abdomen. The birds rounded their backs and extended their wings and tail to completely cover the cup and egg when it rained. Both adults opportunistically caught unidentified flying insects and frequently appeared to pick up small items—which we assume were nest parasites—and eat them during incubation and nestling stages.

Our observations of nest #2 prior to capture of the adult were limited. Following capture, we used radio tracking to monitor incubation patterns. We detected radio signals from both adults coming from nest #2 on 4, 5, and 6 May 2005 but did not approach the nest. On 7 May 2005, we received no radio signal for either adult near the nest; at 1230 hrs, we approached the nest and found it unattended. Closer inspection of the egg revealed a puncture hole ~10 mm in diameter. The puncture was clean, with no fracturing of the shell around the hole. A developing embryo inside the egg was visible through the hole. The inner lining surrounding the embryo had been punctured as well. Neither adult was observed in the nest area following failure of the nest.

TABLE 1. Items fed to a nestling Banded Ground-cuckoo in northwestern Ecuador in 2005.

Food	Category		Subgroup	
	n	%	*n*	%
Vertebrates	12	16.9		
Anurae (frogs)			8	11.3
Anolis sp. lizards			3	4.2
Micrurus sp. coral snake			1	1.4
Invertebrates	39	54.9		
Coleoptera			3	4.2
Lepidoptera			3	4.2
Cicadadae			1	1.4
Orthoptera			23	32.4
Araneae			4	5.6
Unknown arthropods			2	2.8
Oligochatea			3	4.2
Unknown	20	28.2		
Totals			71	100

Nestling Stage and Fate of the First Nest.—The egg in nest #1 hatched between 1800 hrs EST on the evening of 14 March 2005 and 1200 hrs on the following morning, and the chick fledged 20 days later. There was no statistical difference in the rates at which the two adults brooded and fed the nestling. On average, the nestling was brooded 24% of the time by the radio-equipped bird and 33.5% of the time by the unbanded bird (Mann-Whitney U_{38} = 394, P = 0.6). Similarly, the radio-equipped bird fed the nestling an average of 0.34 ± 0.07 times/hr whereas the other adult fed it an average of 0.25 ± 0.06 times/hr (Mann-Whitney U_{36} = 631, P = 0.4). Adults brought a range of vertebrate and invertebrate food items (Table 1) and interacted little at the nest. Both birds continued bringing fresh leaves until the chick fledged.

The chick successfully fledged from the nest at 0950 hrs on 4 April 2005. We observed both parents with the fledgling from 4 April through 8 April 2005. Observing the birds was difficult and we limited our observations of post-fledging care. We did note, however, that both adults were present and continued to feed the fledgling, which appeared dependent on its parents for food and protection. We did not note any begging vocalizations or behavior. We located only the radio-equipped adult, which appeared to be alone, first on 9 April 2005 and then on three subsequent radio-tracking sessions (10, 11, 14 Apr). During the next radio-tracking session (27 Apr) we discovered the radio-equipped bird attending nest #2, which had one egg that was already being incubated. We are uncertain if the fledgling from nest #1 died on 8–9 April, or if the radio-equipped individual left the fledgling in the care of the unbanded adult to start a second nesting attempt with another bird.

Nestling Plumage and Behavior.—The chick's body was covered in white down but its head remained featherless from day 0 (hatching) through day 5. Pin feathers were visible on the chick's head by day 5, and dark feathers were becoming visible beneath the light-colored down on the body. The chick's body was covered equally in down and dark feathers by day 10, a prominent crest was visible on its head, its eyes were open, and it was able to handle and swallow food on its own. The chick was almost entirely covered in dark feathers on day 15 and the skin behind the eye had begun to turn blue. Prior to fledging, it became increasingly active in the nest, eating small insects from within the nest and even catching a flying dipteran with its bill. The chick was entirely covered with a dark plumage similar to that of adults but lacking iridescence when it fledged on day 20, and its crest and the blue skin around its eyes were similar to those of adults. Its beak, however, was noticeably smaller than those of the adults and its tail was less than one-quarter the length of an adult tail.

We did not hear the chick vocalizing while in the nest but it began to snap its bill on day 15. From days 17–20, it did so increasingly when adults were away from the nest (not when they were present). The bill snaps were often answered by bill snaps of adults that were out of our sight but within hearing range.

DISCUSSION

It has been known since the 1940s that ground-cuckoos raise their own young and are not brood parasites (Sick 1949). Prior to the present report, only the nest of the Rufous-vented Ground-cuckoo (*N. geoffroyi*) had been described (Roth 1981) but it was unclear whether one or two adults tended the nest. Here we report the Banded Ground-cuckoo provides bi-parental care with both parents contributing equally to incubation, brooding, and provisioning the nestling. This information in combination with the knowledge the species is monomorphic suggests a monogamous mating system (Andersson 1994).

The known nesting biology of Banded and Rufous-vented ground-cuckoos is quite similar. Both species construct bulky, open cup nests at similar heights in understory trees of the genus *Miconia*, although the Rufous-vented Ground-cuckoo nest was slightly lower (2.5 m above the ground) than the two Banded Ground-cuckoo nests we found (3.9 and 5.4 m above the ground). The Rufous-vented Ground-cuckoo nest contained only one egg. We found both Banded Ground-cuckoo nests during incubation stage and cannot be certain of the original clutch size. However, it appears likely the nests we found also had only one egg each. Finally, the account of juvenile plumage in *N. geoffroyi* provided by T. Howell in Haffer (1977) is similar to the data we recorded. We could find no published description of any other *Neomorphus* nest, but Schönwetter (1964, 1988) reports that Rufous-winged Ground-cuckoo (*N. rufipennis*) eggs are 29.2–32.0 × 37.1–41.5 mm, which is slightly smaller than our size estimates for eggs of the Banded Ground-cuckoo.

Both Banded and Rufous-vented ground-cuckoos regularly replenished their nests with fresh green leaves, a trait also recorded in related cuckoos, such as anis (*Crotophaga* spp.) (Roth 1981). A potential explanation for this practice is that chemical compounds in the leaves suppress nest parasites, such as mites (Whimberger 1984). Another possibility is that decomposition of the thick layer of leaves in the nest may provide an additional source of warmth for the egg and chick, as is the case for some reptiles and ground-nesting birds (Seymour and Ackerman 1980).

No detailed data are available on the diets of any *Neomorphus* Ground-cuckoos, but the diets of the phylogenetically related roadrunners (*Geococcyx* spp.) (Dickinson 2003) are well documented and include a breadth of vertebrates and invertebrates (Bent 1940, Baughman 2003). The Banded Ground-cuckoo pair we studied fed the nestling a wide range of vertebrates and an even wider range of invertebrates (Table 1), which may reflect the composition of the adult diet.

CONSERVATION IMPLICATIONS

The radio-equipped Banded Ground-cuckoo's home range included secondary and altered forest (JK, unpubl. data) but both nests we monitored were built in primary forest. The patch of primary forest with the two nests was surrounded by a complex mosaic of forest types including undisturbed primary forest, selectively logged forests, and 10–15 year-old secondary forest re-growth following intense disturbance. The nests were ~250 m from the edge of the Bilsa Reserve and two major trails ~5 m wide that are heavily traveled by humans and domestic animals including mules, horses, and cattle. At the junction of these two trails, ~350 m from the nests, is a community of four families (La Y-cita), a small store, and a school. Thus, although the habitat immediately surrounding the nests was undisturbed, the area surrounding the patch of primary forest where both nests occurred was far from pristine.

The information on nesting biology presented here highlights the challenges involved with conserving the Banded Ground-cuckoo. One nest failed during the incubation stage and the ultimate fate of the other nesting attempt was uncertain. The species appears to have a small clutch size, perhaps only a single egg. It also may depend on primary rain forest for nest sites, but even when these requirements are met it may be susceptible to more subtle effects of human activities such as hunting, dogs, or edge effects (e.g., Gates and Gysel 1978). The information is scanty, but what little that is known of reproductive biology of other *Neomorphus* spp. raises similar concerns for conservationists. The Scaled Ground-cuckoo (*N. squamiger*) is considered "near threatened" with extinction, has a small range and is reported to be sensitive to human disturbance and encroaching human development (BirdLife International 2000, 2004). The Rufous-vented Ground-cuckoo nest reported by Roth (1981) was in secondary forest, had only a single egg, and failed during incubation stage.

The Banded Ground-cuckoo is one of Ecuador's rarest birds and has potential to serve as a flagship species for conservation efforts in the Chocó. It appears that conservation of large tracts of primary Chocó habitat is necessary for conservation of endangered, endemic species such as the Banded Ground-cuckoo.

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DENSITY AND NATURAL HISTORY OF THE SICKLE-WINGED GUAN (*CHAMAEPETES GOUDOTII*) IN THE CENTRAL ANDES, COLOMBIA

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ABSTRACT.—The basic ecology of most of the Andean guans is poorly known. However, knowledge of the natural history of members of Cracidae has increased in the last decade, but most studies involve lowland species. We present basic natural history data for the Sickle-winged Guan (*Chamaepetes goudotii*) on the western slope of the Central Range of the Andes, Colombia. The density estimate for the Sickle-winged Guan in the study area was 13.7 individuals/km^2 and the mean (± SD) group size was 1.5 ± 0.76 individuals. These groups used all forest strata but usually foraged in the middle stratum (8.6 ± 6.1 m). The diet consisted of fruits (84.5%), flowers (3.9%), leaves (5.8%), and invertebrates (5.8%). We observed wing-drumming displays, nests, and fledglings from January through June. We discuss the ability of the Sickle-winged Guan to colonize and establish populations in restored habitats. *Received 3 April 2006. Accepted 6 September 2006.*

The Sickle-winged Guan (*Chamaepetes goudotii*) is one of the few members of the family Cracidae present at higher elevations (Hilty and Brown 1986, Fjeldså and Krabbe 1990, del Hoyo 1994, Delacour and Amadon 2004). Members of the Cracidae are among the most threatened avian species in the Neotropics as a consequence of hunting, forest fragmentation, and low rates of population growth (Silva and Strahl 1991, Strahl et al. 1997, Renjifo 1999, Brooks and Gonzales-García 2001, Brooks et al. 2001, Mamani 2001, Delacour and Amadon 2004). These factors influence the vulnerability of members of this family to local extirpation (del Hoyo 1994, BirdLife-International 2000, Renjifo 2002). Despite its large geographic distribution, comprehensive ecological studies on the Sickle-winged Guan are not available, and only sporadic observations have been reported (Jonhson and Hilty 1976, Hilty and Brown 1986, del Hoyo 1994, Nadachowski 1994, Greenfield and Ortíz-Crespo 1997, Renjifo 1997, Salaman et al. 2001, Strewe 2001, Pulgarin-R 2004). Little is known about the diet of this guan and nothing is known about densities or population dynamics.

The genus *Chamaepetes* includes two species distributed from Costa Rica to northern Bolivia. The Black Guan (*Chamaepetes unicolor*) has a small range from Costa Rica to western Panama (Stiles and Skutch 1989), whereas the Sickle-winged Guan has a wide distribution in the northern Andes from Colombia, Ecuador, and Peru to northern Bolivia, mostly from 1,500 to 3,000 m elevation (Hilty and Brown 1986, del Hoyo 1994, Delacour and Amadon 2004). There are five described subspecies of the Sickle-winged Guan, with *C. g. goudotii* occurring on our study area. The species was considered widespread in Colombia (Hilty and Brown 1986), but extensive deforestation in the Andean region (Cavelier and Etter 1995) and continued over-hunting have resulted in the placement of this guan on a list of taxa of immediate conservation priority (Brooks and Strahl 2000).

The overall objective of our study was to provide detailed ecological data for Sickle-winged Guans. Specific objectives were to estimate local population densities, document group size, characterize the vertical foraging strata, describe the diet, and identify the timing and length of the breeding season.

METHODS

Study Area.—Our study was conducted at the Santuario de Fauna y Flora Otún-Quimbaya (SFFOQ) (4° 43′ 11″ N, 75° 28′ 70″ W)

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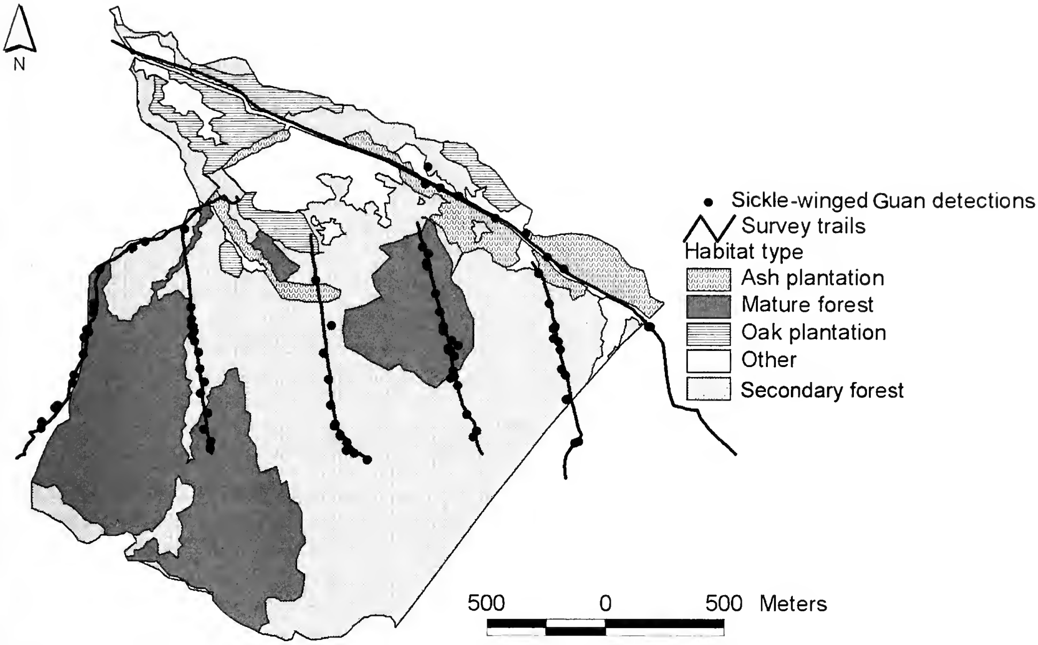


FIG. 1. Sickle-winged Guan detections by habitat types in the Santuario de Fauna y Flora Otún Quimbaya, Colombia, October 2002–September 2003. The vegetation map was modified from Garcia-Robledo and Murcia (2005).

on the western slope of the Central Range of the Andes, east of Pereira, Department of Risaralda, Colombia. The area studied was between 1,900 and 2,100 m elevation. Mean maximum and minimum annual temperatures are 20 and 11° C, respectively. The mean annual rainfall is 270 cm which is bimodally distributed, with dry seasons of <10 cm of rainfall per month occurring during December–January and June–August (Ríos et al. 2005).

The SFFOQ encompasses 489 ha most of which was clear-cut to create pastures for livestock grazing in the early 1900's. The sanctuary has been protected from logging since 1960 (Londoño 1994) and a reforestation strategy was established to restore forests by planting Chinese ash (*Fraxinus chinensis*) and Andean oak (*Quercus humboldtii*), or by allowing natural regeneration. This strategy resulted in the creation of a variety of habitats (Fig. 1). The mature forest that remains occurs as forest patches that were not logged.

Density Estimation and Habitat Use.—We surveyed Sickle-winged Guans from trails that passed through all forested habitat types and most plantations within the study area (Fig. 1). The distance of survey trail in each forest habitat was similar to habitat availability (Table 1). We conducted monthly surveys on six 1-km trails from October 2002 to September 2003.

TABLE 1. Scale of habitat availability (ha) and habitat used (survey distance = m) by Sickle-winged Guans in the Santuario de Fauna y Flora Otún Quimbaya, Colombia, October 2002–September 2003.

Habitat type	Habitat availability (%)	Survey distance (%)	Habitat used (df = 2)
Secondary forest	253.8 (51.9)	3,175 (50.7)	$\chi^2 = 0.08$, $P = 0.77$
Mature forest	138.9 (28.4)	1,650 (26.3)	$\chi^2 = 1.29$, $P = 0.26$
Oak plantation	14.6 (3.0)	75 (1.2)	
Ash plantation	33.7 (6.9)	1,300 (21.9)	$\chi^2 = 2.01$, $P = 0.16$
Others	48 (9.8)		

Each trail was surveyed eight times per month, four times in the morning (0630–0830 hrs EST) and four in the afternoon (1530–1730 hrs). We conducted 48 surveys per month for a total of 576 during the year. We used visual detections for estimating densities. We recorded wing-drumming displays during the breeding period but did not include these in density estimates because birds appear to move constantly during the wing-drumming display creating a potential bias in perpendicular distance estimations. We estimated the perpendicular and vertical distances from the trail to each guan detected. We quantified the length of the survey trails that covered each habitat type to estimate habitat use. We estimated the number of guans according to availability of each habitat based on the total guans detected on surveys.

Statistical Analyses.—We estimated guan density using the distance sampling approach in program DISTANCE v 4.1 (Buckland et al. 2001). This program diminishes bias created by environmental conditions and differences among observers (Thompson 2002). Guan density estimates were obtained by selecting the best model included in the program based on Akaike's Information Criterion (AIC). The model also considers the probability of detection, encounter rate, and cluster size. The probability of detection in our study was higher in the forest compared to the ash plantation but encounter rate and cluster size were higher in the ash plantation. We used a one-way analysis of variance (ANOVA) to examine whether there was variation in monthly densities. We used a Chi-square test to examine if guans were using different habitats according to their availability. Observation time and number of surveys per trail were standardized; thus, survey effort was considered in habitat-use estimation.

Fruit Availability.—Quantification of fruit available on the study site was measured by randomly placing three 50 × 4 m plots along each of the six trails where guan surveys were conducted (Fig. 1) for a total of 18 plots. Trees with >3 cm DBH were marked with uniquely numbered aluminum tags. We made direct observations every 15 days for each tree when trees where fruiting. We counted the total fruits available on at least two branches and then counted the number of branches with fruits to obtain the total fruit available on each tree (Blake et al. 1990). We estimated total fruit available on each tree by multiplying the average number of fruits from the two or more branches with direct fruit counts by the total branches with fruit. Species identifications were made using field guides (Vargas 2002) and by comparing samples from the study area with specimens in the botanical museums of Colombia.

Natural History.—We collected natural history data during our 576 surveys and observations from June 2002 to December 2003 during continuous searches on the SFFOQ trail system. These searches occurred from 0600 to 1800 hrs for 10 days each month. We followed guans continuously after finding them as long as individuals and topography allowed. Natural history data collected included: food items eaten, evidence of reproduction, number of sun or dust baths taken, and group size. We recorded only one event per group encounter in the case of the different behaviors, (e.g., if two individuals where feeding on a *Dendropanax* tree, this event was counted as one observation).

We categorized non-adult Sickle-winged Guans as: (1) fledglings—individuals that did not have a tail or had their body covered with down and one-third of adult size, (2) juveniles—individuals with body feathers and a tail, but wing feathers were not fully grown and measured two-thirds of adult size, and (3) subadults—with more adult-like plumage, but less colorful and somewhat smaller than adults.

Observations by German Corredor of captive Sickle-winged Guans in the Cali Zoological Park suggested that males and females can be differentiated by morphological characters. Our field data support this observation. We differentiated male and female Sickle-winged Guans based on both morphology and behavior. Males gave wing-drumming displays and had bright blue skin around the eye, whereas females incubated eggs and had blackish skin around the eye. This has not been previously reported. However, future molecular studies between and within subspecies are needed to see if this is true and applies to the different subspecies.

RESULTS

Density and Habitat Use.—The density estimate for Sickle-winged Guans in the study

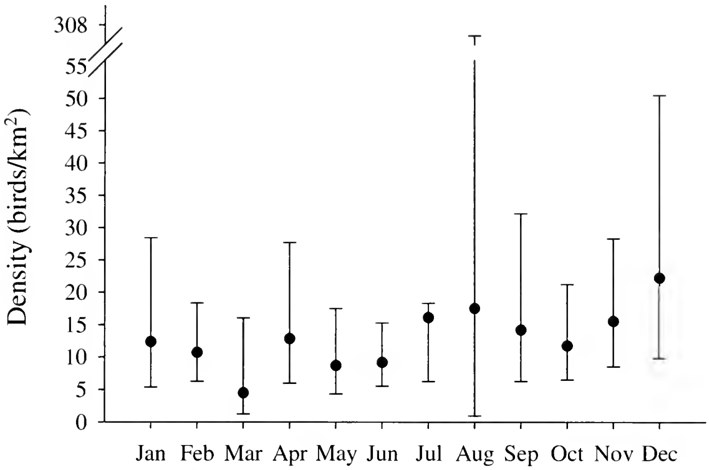


FIG. 2. Density variation of Sickle-winged Guans in the Santuario de Fauna y Flora Otún Quimbaya, Colombia between October 2002 and September 2003. Bars represent 95% confidence intervals, dots = means.

area was 13.7 individuals/km^2 (95% CI = 9.95–17.12). Monthly mean density estimates varied between 4.5 and 22.3 individuals/km^2 (Fig. 2), but there were no differences among months due to high within-month variation (F = 3.078, P = 0.419). Fruit availability did not explain guan density variation when the species' specific fruit preference was considered (r^2 = 0.389, P = 0.211) or when compared to fruit preferences of other cracids in the study area (r^2 = 0.155, P = 0.631). We estimated expected habitat use detections (n = 141) of guans during the surveys based upon the availability of each habitat on the survey trails. The observed habitat use of the Sickle-winged Guan did not differ from that expected based on habitat availability (Table 1).

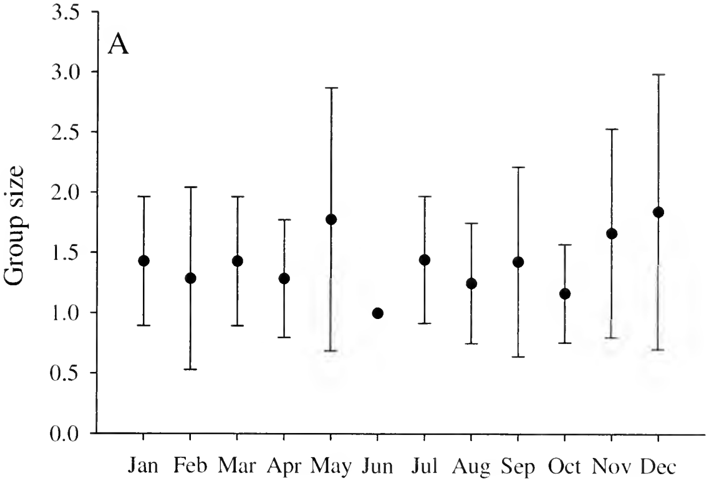
Group Size and Foraging Height.—Group size ranged from one to four individuals and mean (± SD) group size was 1.5 individuals (± 0.76). Mean group size was similar between months (Fig. 3A). Sickle-winged Guans traveled mainly in the middle vertical stratum of the forest (8.6 ± 6.1 m), but used all vertical strata over the course of the year (Fig. 3B). Guans detected on the forest floor were taking a dust bath, following army ants (*Labidus praedator*), or with fledglings.

Diet.—We observed Sickle-winged Guans consuming a variety of foods including fruits, flowers, leaves, and invertebrates (Table 2). Fruit was the most common item (83.8%) eaten, followed by leaves (7.4%), invertebrates (5.9%), and flowers (3.0%) during 68 different foraging observations. Analysis of 25 fecal samples yielded similar results (88% contained fruit with 4% for each of the other three categories). All seeds (ranging in size from 0.1 to 28.3 mm) in fecal samples appeared undamaged, indicating that guans facilitate seed dispersal. Forty-four percent of the fruit in the diet consisted of *Oreopanax* aff. *floribundum* (Araliaceae; recorded only during Dec) and *Aniba muca* (Lauraceae; consumed from Mar to Oct). Consumption of invertebrates occurred only while guans were following army ants during September, October, and November. We had only five observations of guans following army ants and four involved a single individual; the other observation was of a group of two individuals.

Reproduction.—We recorded evidence of reproductive activity from January to June. Wing-drumming displays were heard 39 times during this period with 84.6% occurring from March through May. Most (56.4%) of the wing-drumming detections occurred between sunrise and 0800 hrs EST. A pair was observed closely on 29 May 2003 as the male performed a wing-drumming display. The male repeatedly flew from high to low trees with the tail open and was followed by the female. We observed the male give wing-drumming displays over a period of 5 min separated by intervals of about 1 min within an area of about 100 m. Similar wing-drum-

TABLE 2. Foods consumed by the Sickle-winged Guan in the Santuario de Fauna y Flora Otún Quimbaya, Colombia. October 2002–September 2003.

			Fruit size (mm)		
Species	Categories	Diet (%)	length	width	Month
Araliaceae					
Dendropanax macrophyllum	Fruit	3.8	7.6–12.5	9.2–13.8	May, Jun
Oreopanax aff. *floribundum*	Fruit	18.0	4.8–8.9	7–8.3	Dec
Arecaceae					
Prestoea acuminata	Fruit	2.8	10–12.5	8.8–12.1	Oct
Wettinia kalbreyeri	Flower	0.9			Oct
Asteraceae					
Unknown	Fruit	0.9			Nov
Clusiaceae					
Chrysochlamis colombiana	Flower	1.9			Apr
Euphorbiaceae					
Alchornea grandiflora	Fruit	3.8	5.3–9.3	4.2–10.1	Feb, Mar
Allophylus mollis	Fruit	1.9	8–10.5	7.7–12.1	Aug
Lauraceae					
Aniba muca	Fruit	17.0	14.1–33.6	15.5–18.4	Mar, Apr, Sep, Oct
Lycaria sp.	Fruit	0.9			Aug
Nectandra lineatifolia	Fruit	0.9	10.8–17.5	7–12.6	Aug
Melastomataceae					
Henriettella trachyphyla	Fruit	0.9			Apr
Miconia acuminifera	Fruit	4.7	5.9–9.5	5.8–10.4	Sep, Oct, Nov
Miconia theaezens	Fruit	1.9	3–6.2	3.6–6.8	Oct
Miconia aff. *resima*	Fruit	1.9	4.3–8.1	6.5–8.8	Oct, Nov
Moraceae					
Cecropia telealba	Fruit	4.7	126.6–270	13–31.6	Mar, Apr, Oct
Ficus andicola	Fruit	1.9	7–9.1	9–20.5	Oct
Ficus mutisii	Fruit	0.9	19.2–24.4	20.3–28.5	Jan
Ficus sp. # 1	Fruit	0.9			Dec
Ficus sp. # 2	Fruit	0.9			Sep
Oleaceae					
Fraxinus chinensis	Leaf	4.7			Nov, Dec
Chionanthus sp.	Fruit	5.7			Oct
Rubiaceae					
Palicourea angustifolia	Fruit	3.8	5–10	5.2–11.7	Mar, May, Jun
Palicourea ovalis	Fruit	0.9	10.5–13.5	10.1–13	Jul
Coussarea sp.	Fruit	0.9	6.6–10.5	7.8–12.7	Jul
Solanaceae					
Lycianthes radiata	Fruit	0.9			May
Solanum sycophanta	Flower	0.9			Oct
Symplocaceae					
Symplocos quinduensis	Fruit	3.8	9–14.2	5.6–9.6	Apr, May
Unknown					
Unknown sp. # 1	Leaf	0.9			Jun
Unknown sp. # 2	Invertebrate	5.7			Sep, Oct, Nov



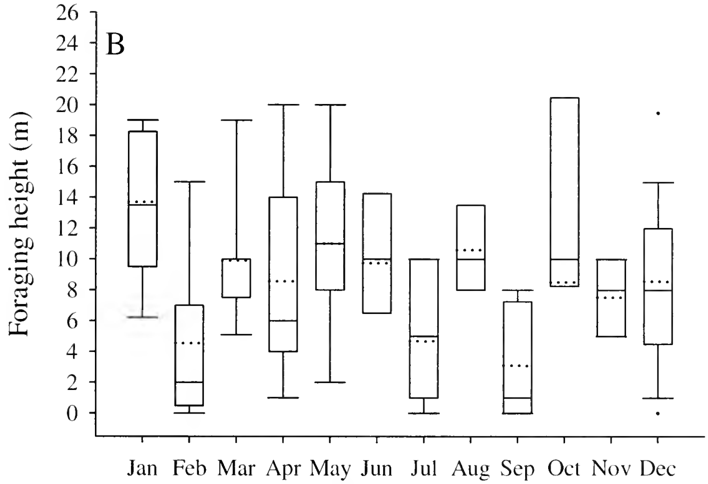


FIG. 3. Vertical foraging stratum and group size of Sickle-winged Guans in the Santuario de Fauna y Flora Otún Quimbaya, Colombia between June 2002 and December 2003. (A) Group size variation; dots represent the mean and bars the standard deviation. (B) Foraging stratum used; the box plots represent the 95% confidence intervals from the number of individuals observed in each month. The number of guans observed per month is shown by the solid line (median) and the dotted line (mean).

ming behaviors were observed on five additional occasions for shorter periods of time.

We found two nests each positioned on epiphytic plants and constructed using materials found on the epiphytic plant. We found the first nest on 29 June 2002 when a female flew from a bromeliad 4 m above the ground. This nest contained a recently hatched white egg shell, with fresh egg membranes. The female flew in circles around the nest making alarm calls during our presence indicating a chick was probably close to the nest. The second nest was 6 m above ground on an epiphyte (*Anthurium glaucospadix*, Araceae) and was found on 6 May 2003 when a female flew from the epiphyte, exposing two white eggs among its branches and leaves (Fig. 4A). The nest was visited 3 days later, and one of the eggs was broken and contained a dead well-developed embryo covered with natal down. The unbroken egg measured 73.7 × 51.8 mm and weighed 96.8 g (Fig. 4B). Due to the absence of the female from the nest prior to finding of the broken egg, we assume the nest was abandoned. We do not believe that predation was the cause as none of the eggs was missing.

The unbroken egg was artificially incubated and hatched 7 days later. The fledgling weighed 68.3 g and was totally covered with rufous down except for the wings, which had black feathers with two rufous bars. Three black lines extended through the upper part of the body. Two lines were narrow extending from the bill along the sides of the head through the flanks to the end of the body. The other was a wider line running dorsally from the upper head to the tail. The bill was completely black, the eyes brown, and the legs pink. It had a dark patch of bare skin around the eye and did not have a tail. We fed the fledgling with worms and fruits, and its weight increased 74.8 g in 7 days (Fig. 4C).

We encountered fledglings six times, three in April, one in June, and two in July. Both adults were seen with the chick on one of these occasions, whereas the other observations involved only the female. During these encounters, females accompanying fledglings produced constant alarm calls and flew in circles around the area where the fledglings were hidden. This behavior lasted as long as observers were present in the area. When the male was present, he performed the wing-drumming display. We observed juveniles on three occasions, one in September and two in June. One subadult was observed in December 2002 with both parents; this individual was smaller than the adults but had adult-like plumage.

DISCUSSION

Density and Habitat Use.—The Sickle-winged Guans on our study area occurred at higher densities compared to other cracids (Terborgh et al. 1990, Galetti et al. 1997, Strahl et al. 1997, Brooks and Gonzáles-García 2001). This is surprising given the relatively large amount of successional forest in the SFFOQ. The importance of habitat heterogeneity for food availability, nesting sites, and movement has been documented for other cracids (Strahl et al. 1997, Santamaria and Franco 2000, Brooks and Gonzales-García 2001, Parra et al. 2001). Habitat heterogeneity also created temporal variation in fruit availability both between and within habitats, and influenced movements of Salvin's Curassows (*Mitu salvini*) (Santamaria and Franco 2000, Parra et al. 2001). A factor potentially influencing the density of guans on our study area was the connection of the SFFOQ to the heavily forested Ucumari Natural Reserve. This large (3,980 ha) reserve could be an important source region for Sickle-winged Guans.

We observed Sickle-winged Guans in all forest types available within our study site and one of the ash plantations. This guan seems to be a habitat generalist, as all habitats were used in proportion to their availability. The use of secondary forest and plantations is important for population growth and colonization of restored areas within a fragmented landscape.

Group Size and Foraging Height.—Guans were mostly observed alone or in pairs traveling in the middle strata of the forest. We observed few family groups in contrast to reports from other sites where groups of up to eight individuals have been detected in fruiting trees (Salaman et al. 2001). Our observations agree with most of the previous group sizes observed for members of this family (Delacour and Amadon 2004).

Delacour and Amadon (2004) suggested that *C. goudotii* is mainly terrestrial, but most of our detections were of individuals in trees supporting the idea this guan is mainly arboreal (Johnson and Hilty 1976, Hilty and Brown 1986, Remsen and Cardiff 1990). Sickle-winged Guans were detected on the forest floor but most of these records corresponded to individuals capturing invertebrates while following army ants. Sickle-winged Guans are large and heavy, which may reduce maneuverability in trees and their ability to capture invertebrates or other animals. Use of the forest floor can be important for acquisition of protein-rich invertebrates (Robert et al. 1995, Klasing 1998). Cracids have been reported as rare army ant followers (Willis and Oniki 1978). Guans were among the birds most frequently detected at army ant swarms at our study site, where "professional" ant-following species are absent. There are no previous records of Sickle-winged Guans and few records of other cracids, as ant followers in highland habitat (Vallely 2001); one exception is the Cauca Guan (*Penelope perspicax*) within our study area (Rios et al. 2006).

Diet.—Previous reports of the diet of Sickle-winged Guans have concluded that fruits,

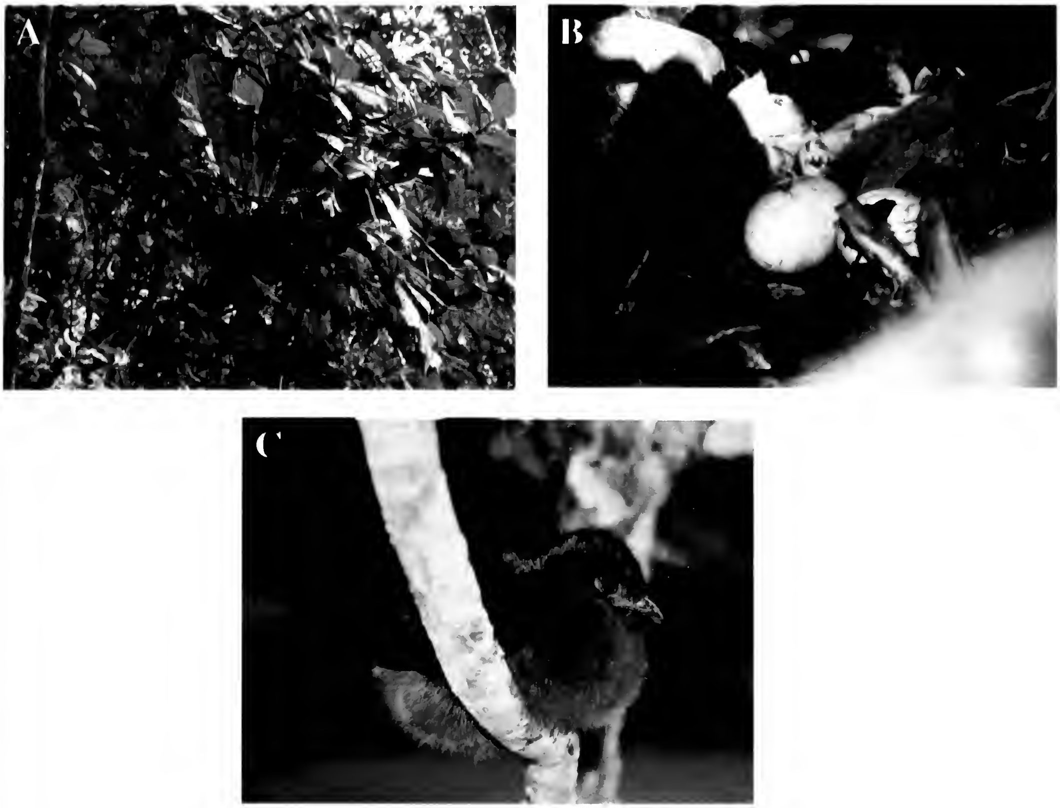


FIG. 4. Reproductive evidence of Sickle-winged Guans in the SFFOQ during June 2002 to December 2003. (A) Nest in an epiphyte (*Anthurium* sp.) on 6 May 2003. (B) Eggs in Sickle-winged Guan nest on 6 May 2003. (C) One-week-old Sickle-winged Guan chick hatched from egg found on 6 May 2003.

leaves, and flowers are the most important food items (Johnson and Hilty 1976, Ridgely and Gaulin 1980, Cardiff and Remsen 1981, Remsen and Cardiff 1990, Nadachowski 1994, Renjifo 1997). We also observed the diet of Sickle-winged Guans mainly consists of fruits, similar to what has been reported for other members of the Cracidae family (Galetti et al. 1997, Strahl et al. 1997, Santamaría and Franco 2000, Brooks and Gonzales-García 2001). Sickle-winged Guans ate a variety of fruit (24 species) but fed mostly on *A. muca* (Lauraceae) and *O.* aff. *floribundum* (Araliaceae). The lipid content of *A. muca* is low (2.8%). In contrast, *O.* aff. *floribundum* has a high lipid content (27.2%) compared with other items in the diet (Muñoz 2003) and other neotropical fruits (Moermond and Denslow 1985). The large difference in lipid content between the two major fruits eaten by Sickle-winged Guans suggests that other factors are also important in fruit selection (e.g., availability of other items, physiological requirements). Although these two trees are not abundant in the area (M. M. Rios et al., unpubl. data), they provided an important food resource during a low fruit production period in our study (Muñoz 2003).

Fruits are generally low in protein and lipids in contrast to seeds and invertebrates (Klasing 1998). The Sickle-winged Guan does not eat seeds and must consume invertebrates to gain the protein lacking in fruits. Invertebrates accounted for a small percentage (5.4%) of the diet, but likely contained sufficient protein to meet nutrition requirements (Morton 1973, Moermond and Denslow 1985, Karasov 1990). Invertebrates are regularly reported in the diet of terrestrial cracid species (Sermeño 1997, Santamaría and Franco 2000, Jiménez et al. 2001), but there are few reports of invertebrate consumption by arboreal guans

(Strahl et al. 1997, Brooks and Gonzales-García 2001, Muñoz 2003). This could be a result of the short time period over which feeding observations are usually gathered or the difficulty in detecting consumption of invertebrates.

Reproduction.—Reproductive information on cracids is scarce (del Hoyo 1994, Strahl et al. 1997, Brooks and Gonzales-García 2001, Delacour and Amadon 2004). Most reported nests of *Chamaepetes* have been built on and with epiphytic plants (Hilty and Brown 1986, Stiles and Skutch 1989, Greeney 2005, this study) in contrast with lowland cracids that use small branches and vines as nesting material (González-García 1997, Santamaria and Franco 2000, Delacour and Amadon 2004). Nests of other highland guans were also found in places where epiphytes are concentrated (González-García 1997). Previous observations suggest that cracids do not transport materials to build their nests (del Hoyo 1994, Nadachowski 1994, Silva 1996, González-García 1997, Santamaria and Franco 2000, Mamani 2001, Delacour and Amadon 2004). Epiphytic plants may have an important role in habitat selection by highland cracids by providing nesting sites because availability of locations with thick vines and lianas that lowland species use for nesting is reduced in the highlands (GAL, pers. obs.). However, there are reports of some highland guan species building nests with vines and branches (Salaman et al. 2001, Rios et al. 2006). If epiphytic plants have an important role in reproduction of highland cracids, this may suggest that old-growth habitat and well established secondary growth habitats are important for reproduction, as younger habitats and ash plantations are unlikely to have many epiphytic plants. During our study we did not record a male performing the wing drumming display in younger habitats or ash plantations, suggesting that Sickle-wing Guans may not use these habitats for nesting. More information is needed to evaluate the importance of epiphytic plants for nesting of highland guan species.

Our observations suggest that incubation in *C. goudotii* is only by the female as reported previously for other cracids (Mamani 1997, Sermeño 1997, Santamaría and Franco 2000). The eggs we found were different in color and pattern than those reported by Salaman et al. (2001) which were covered with fine pale brown speckles, but similar to those reported by Hilty and Brown (1986), Nadachowski (1994), Strewe (2001), and Delacour and Amadon (2004). Our data suggest the breeding season of *C. goudotii* occurs from January to July in the SFFOQ, as has been reported elsewhere for Sickle-winged Guans in the northern Andes (Hilty and Brown 1986, Fjeldså and Krabbe 1990, del Hoyo 1994, Salaman et al. 2001, Strewe 2001, Pulgarin-R 2004), and overlapping with the peak in reproduction of the entire bird community in the area (Naranjo 1994).

The information on appearance of Sickle-winged Guan fledglings available in the literature is ambiguous. Our observations are concordant with the description by Fjeldså and Krabbe (1990) but contrast with the account of Salaman et al. (2001) and Greeney (2005), who described fledglings as being sooty black, except for the head, which is glossy black with a buff lateral crown stripe that extends to the edge of the mantle, but does not merge. Most of the fledglings and juveniles we observed were accompanied by females and only occasionally by males, suggesting that females have a greater role than males during incubation and fledgling periods.

Future studies of this species should focus on nesting requirements, diet, and movements to better understand how current and future fragmentation events (or habitat restoration) may affect population density and movements (Latta et al. 2005). Comparative studies on reproductive success between Sickle-winged Guan populations in restored and mature continuous forest are also needed.

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SUNLIGHT ON FEATHERS INHIBITS FEATHER-DEGRADING BACTERIA

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ABSTRACT.—We studied the effect of sunlight (280–750 nm) on *Bacillus licheniformis*, a feather-degrading bacterium that commonly occurs in the plumage of birds. Colony-forming units (a measure of bacterial abundance) of *B. licheniformis* were numerous on feathers inoculated with *B. licheniformis* and shielded from all sunlight, whereas colony-forming units were significantly less common on inoculated feathers exposed to full spectrum sunlight and sunlight from which the shorter ultra-violet wavelengths were blocked. Sunlight appears to inhibit the growth of feather-degrading bacilli. Given that many avian species sun themselves and that feather-degrading bacilli occur commonly in avian plumage, we suggest that regulation of potentially harmful plumage microorganisms through exposure to sunlight could be one reason that birds sunbathe. *Received 11 October 2005. Accepted 2 September 2006.*

Sun-bathing is a conspicuous maintenance behavior of birds with several possible explanations. Simmons (1986) suggested that sunning is important in thermoregulation and synthesis of vitamin D from uropygial oil. Blem and Blem (1993) suggested that sunning is important for drying wet plumage, and Moyer and Wagenbach (1995) found that sunning dislodges ectoparasites such as lice, mites, and fleas. Black Noddies (*Anous minutus*) endured heat stress as temperatures on the wing feathers during sunning reached 63.4 ± 0.9° C, which caused feather lice to abandon their refuges between the barbs thereby exposing themselves to removal by preening (Moyer and Wagenbach 1995). We suggest that exposure of feathers to sunlight during sunning may inactivate or inhibit feather-degrading bacilli thereby limiting the damage such bacteria cause to the plumage of birds (Burtt and Ichida 1999, Muza et al. 2000).

Bacillus licheniformis is a common soil-dwelling bacterium that degrades feathers (Williams et al. 1990). It occurs in the plumage of 23 (Burtt and Ichida 1999) to 59% (Whitaker et al. 2005; Burtt et al., unpubl. data) of wild birds. *B. licheniformis* is thermophilic and able to sporulate under adverse conditions such as extreme heat and desiccation (Setlow 1995). Thus, it can resist the intense heat of sunning, but its ability to tolerate exposure to solar ultra-violet (UV) and visible radiation during sunning is unknown. Previous studies of UV resistance in *Bacillus* spp. (Nicholson 1995, Setlow 1995) have been based on a ~254 nm laboratory source of ultra-violet radiation, although the earth's surface is shielded from UV-C (200–280 nm) by the ozone layer (Koller 1965). Furthermore, Setlow (1995) and later Slieman and Nicholson (2000) focused almost exclusively on *Bacillus subtilis*, which degrades feathers poorly or not at all. We studied the effect of sunlight (280–750 nm) on growth of feather-degrading *Bacillus licheniformis* by assessing the viability of bacilli sprayed on domestic goose (*Anser anser*) feathers and exposed to sunlight.

METHODS

The experiment was conducted in summer 2003 and repeated in summer 2004 with an additional control for evaluating structural damage to feathers from UV alone. Differences between the experiment and its replication are detailed as necessary. We used white contour feathers of nearly uniform length (~4 cm each) randomly selected from a collection of similar goose feathers to test the effect of sunlight on *B. licheniformis*. We sterilized three (2003) or four (2004) Fisherbrand Redi-tip pipette boxes (13 × 10 cm) with 70% ethanol and mounted eight similar feathers with no visible damage onto the sides of each box (Fig. 1).

The feathers remained suspended without overlap or contact from other feathers or the

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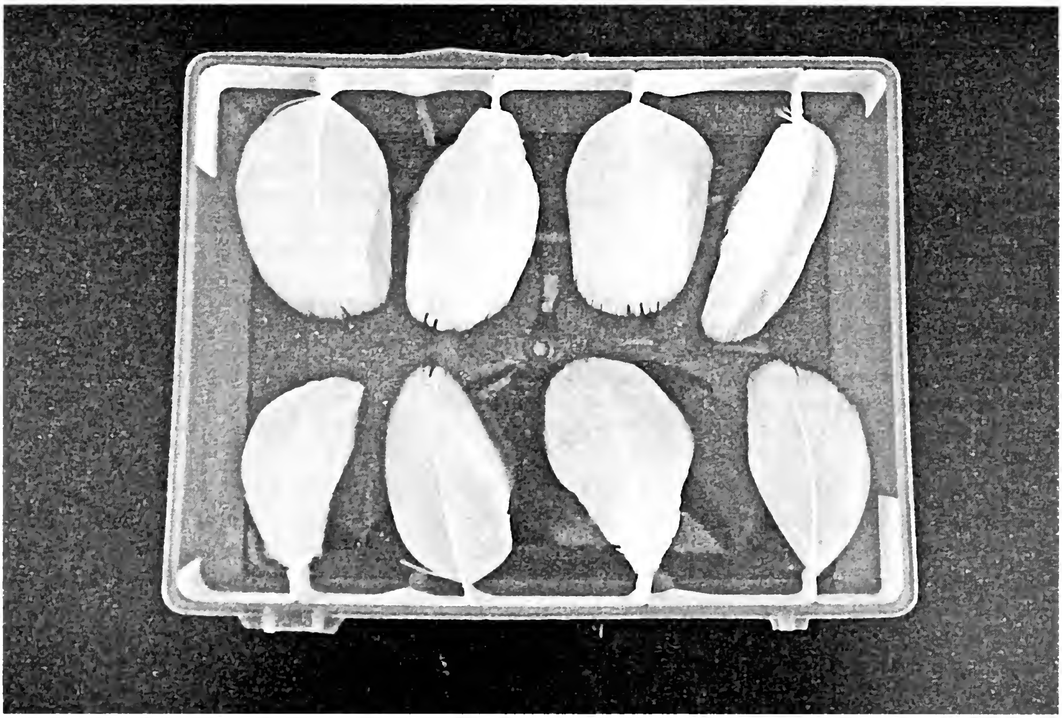

FIG. 1. One of the four boxes that were mounted with domestic goose feathers before inoculating with *B. licheniformis* and prior to attaching the filter.

sides of the boxes throughout the experiment. The boxes with mounted feathers were sterilized at 121° C and 1.3 kPa for 15 min in sealed envelopes to prevent subsequent contamination. We inoculated a Trypticase Soy Agar (TSA; Acumedia, Troy, MI, USA) plate with *B. licheniformis* (strain OWU138B, ATCC# 55768) using a sterile inoculating loop in a laminar flow hood. After 48 hrs of incubation at 37° C, we removed several bacterial colonies from the plate and suspended the bacteria in sterile, physiological saline (0.85% NaCl). We adjusted the turbidity of the bacterial suspension by visually matching it to a 1.0 MacFarland standard ($\sim 3 \times 10^6$ cells ml^{-1}; MacFarland 1907). We transferred the suspension into a sterile atomizer in a laminar flow hood and inoculated four sterile TSA plates with the suspension in the atomizer. We incubated the plates at 37° C and stored the suspension at 4° C to prevent changes in bacterial concentration. Colonies of *B. licheniformis* were present on all plates after 48 hrs; we inoculated all feathers in all three boxes in 2003 and three of four boxes in 2004 as uniformly as possible with the bacterial suspension in the atomizer. We agitated the suspension before spraying with a sterilized magnetic stir bar (VWR Scientific, Marietta, GA, USA) to ensure homogeneity of the bacterial suspension. We applied similar pressure on the atomizer for the same length of time, assuming that an equivalent amount of bacterial suspension would be sprayed onto each feather, if the flow through the nozzle was constant.

We covered the boxes with sterilized glass plates ($\sim 15 \times 15 \times 0.2$ cm). One box was covered with a SCHOTT WG280 Ultra-Violet (UV) filter (BES Optics, Warwick, RI, USA) that transmitted UV-B (280–320 nm) and UV-A (320–400 nm) radiation, as well as visible (400–750 nm) light. This filter transmitted ~92% of the incident solar UV radiation, when measured with a digital UVX Radiometer (UV Products, Upland, CA, USA) equipped with a short-wave sensor. The feathers in this box were inoculated with feather-degrading bacilli. A second box was covered with ordinary glass, which transmits sunlight from 320 to 750 nm (Gibson and McNicholas

1919, Summer 1962). Ordinary glass excludes the shorter wavelength UV-B radiation (Koller 1965). Thus, the inoculated feathers in this box were a control for the effect of UV-B on *B. licheniformis*. This filter transmitted ~70% of the incident solar UV. A third box was covered with a plain glass filter coated with multiple layers of white enamel paint and, hence, opaque to both UV and visible sunlight. The inoculated feathers in this box were a control for the potential effect of (full spectrum) sunlight on *B. licheniformis*. This filter transmitted <1% of the incident solar UV. In 2004, a fourth box covered with a SCHOTT WG280 UV filter served as a control for potential structural damage to feathers from solar UV (Bergmann 1982). The feathers in this box were not inoculated with feather-degrading bacilli. We attached the glass plates to the sides of the boxes with masking tape to prevent them from sliding during transport, but in such a manner as to allow air to circulate to the aerobic *B. licheniformis*.

We filled all boxes to a depth of 1 cm (~200 ml) with sterile, deionized water (18.2 MΩcm) to maintain a constant 100% relative humidity. We periodically replenished the water lost due to evaporation. The water level was well below the feathers, but might have occasionally touched the feathers when we moved the boxes. The glass filters differ in their transmission properties only for solar UV and visible sunlight, and not for solar infrared radiation. Thus, similar temperatures were maintained in all boxes during exposure. Moreover, *B. licheniformis* is thermophilic and able to withstand extreme heat and desiccation through sporulation (Setlow 1995). It would not be adversely affected by the high temperatures that could be generated from the greenhouse effect within the boxes. If, in fact, differential temperatures within boxes had induced different proportions of bacilli to sporulate, such variation would disappear once the spores returned to the vegetative state in the incubator. The number of colony-forming units surviving differential exposure to UV would reflect the true proportion of viable bacilli on the feathers. Thus, the design of the experiment was unaffected by potential effects of temperature and humidity.

We exposed all boxes to the sun daily for ~6 hrs (centered about solar noon) in Branch Rickey stadium (Ohio Wesleyan University, Delaware, OH, USA; 40′ 18″ N, 83′ 04″ W) from 17 June 2003 to 18 July 2003 and from 28 June 2004 to 29 July 2004, even in inclement weather. The position of each box relative to the others was switched daily. We recorded both the UV index (Environmental Protection Agency, USA) and the weather condition (National Oceanic and Atmospheric Administration, USA) at hourly intervals during the exposure time. We also recorded the intensity of the solar UV radiation incident on the glass filters with a digital radiometer. The mean incident solar UV intensity (measured at the surface of the filters affixed to the boxes) and mean UV index were 68.00 ± 3.32 $\mu W/cm^2$ and 7.00 ± 0.12, respectively (for both years together), with a UV index between 8 and 10 being "very high" and 6–7 being "high" (Environmental Protection Agency http://www.epa.gov/sunwise/uviscale.html). We chose a location that was free from shadows and other obstructions. When not exposed to the sun (~18 hrs/day), the boxes were incubated at 37° C in complete darkness to prevent any possibility of photo-reactivation of damaged bacteria (Freidberg et al. 1995).

Water absorbs short wave UV radiation and scatters longer wavelength UV radiation (Koller 1965). Due to evaporation, large droplets of water (4–8 mm diameter) condensed on the underside of the glass plates. If left untreated, the droplets would absorb incident short-wave solar UV and reduce the dosage of UV reaching the feathers. We gently tilted the boxes every hour during exposure, to make the condensed water flow back into the box to minimize attenuation of solar UV by the droplets. We recorded the condensation on each filter as approximate surface area coverage and this value monotonically decreased after the above procedure was performed once or twice. We ensured that water flow was along the surface of the filter to the sides of the boxes to prevent the water droplets from falling on the feathers and washing off the bacteria. We do not believe that erratic dripping could have occurred as the boxes were left undisturbed in the sun and the droplets were not allowed to aggregate to a size sufficiently large to drip from their own weight. There is no reason to suspect that erratic dripping washed the inoculum from feathers of one

TABLE 1. Occurrence of *B. licheniformis* on feathers subjected to differential exposure to sunlight in 2003 and 2004 (Delaware, OH, USA).

	Mean (± SE) number of *B. licheniformis* colony-forming units/feather		
Exposure conditions	2003	2004	Overall
280–750 nm	0.67 ± 0.33	72.63 ± 27.35	53.00 ±.20.92
320–750 nm	3.83 ± 1.89	113.81 ± 37.24	83.82 ± 28.89
No sunlight	300.00 ± 0.00	275.13 ± 12.21	281.91 ± 9.12
One-way ANOVA, df = 2	n = 3/condition, $P < 0.001$	n = 8/condition, $P < 0.001$	n = 11/condition, $P < 0.001$

treatment more than those of others, given that we did not observe differential condensation within the different treatment boxes.

At the end of the experiment, we dismantled the setup and stored the boxes with the feathers still attached at 4° C, for further study. In 2003, three feathers were chosen at random from each treatment and used to inoculate 18 sterile Trypticase Soy Agar (TSA) plates, two plates for each of the three feathers from the three boxes. The rest were used for scanning electron microscopy (SEM). The feathers were held with flame-sterilized forceps and the dorsal and ventral surfaces were streaked multiple times across TSA plates to inoculate the media. We ensured the vane of the feather contacted the surface of the agar, judging from feather impressions. In 2004 we cut a small distal portion (~15 × 2 mm) from every feather in all four boxes using a clean scalpel fitted with sterile blades and stored the distal pieces at 4° C for SEM analyses. We placed the remaining portion of each feather in a separate, sterile test-tube containing 10 ml sterile physiological saline and removed *B. licheniformis* by shaking them on a vortex shaker (Vortex-Genie 2, Scientific Industries Inc., Bohemia, NY, USA) for 30 sec. We used sterile pipettes to inoculate 64 sterile TSA plates (two plates for each feather) with three drops (~0.1 ml) of each of the 32 suspensions (one suspension per feather from four boxes each containing eight feathers) and evenly spread the drops using sterile inoculating loops. We incubated the inoculated plates at 37° C for 48 hrs and counted the *B. licheniformis* colonies, which were easily identifiable by their distinct wrinkled, cone-shaped morphology (Claus and Berkeley 1986). We used Minitab, release 14 (Minitab Inc., State College, PA, USA) to perform one-way ANOVA and *t*-test with α equal to 0.05.

RESULTS

There was no visible damage to the rachis, barbs or barbules of our uninoculated control feathers from exposure to full spectrum sunlight (280–750 nm). There was no visible damage among inoculated feathers exposed to full spectrum sunlight or those exposed to sunlight from which the UV-B (280–320 nm) was blocked. The SEM revealed damage to the barbs and barbules, but nothing that corresponded to the pattern of exposure to UV and visible sunlight.

No *B. licheniformis* grew on cultures from control feathers that were not inoculated with bacilli, but exposed to sunlight with UV-B radiation (280–750 nm). We found no significant differences in the occurrence of *B. licheniformis* for a given treatment between years (paired $t = -1.29$, $P = 0.33$), therefore we combined the data for 2003 and 2004. The occurrence of *B. licheniformis* among feathers subjected to differential treatments in 2004 mirrored that in 2003 (Table 1).

The number of *B. licheniformis* colony-forming units (CFUs; a measure of viable bacterial density) was significantly greater on cultures from feathers that were completely screened from sunlight than on those from feathers that were exposed to either full (280–750 nm) or partial (no UV-B 320–750 nm) sunlight (one-way ANOVA, n = 11 per treatment, df = 2, $P < 0.001$; Fig. 2). Cultures from control feathers completely screened from sunlight had a significantly greater number of *B. licheniformis* CFUs when compared separately to those from feathers exposed to full (Tukey simultaneous tests, $T = 7.5786$, P

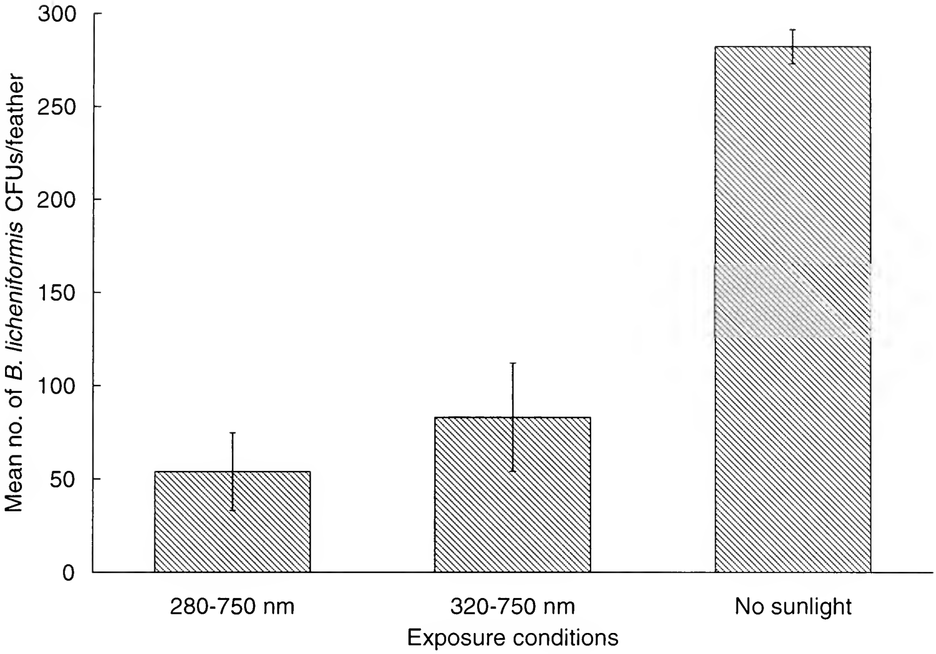

FIG. 2. Occurrence of the feather-degrading bacilli, *B. licheniformis*, on feathers exposed to UV-B, UV-A, and visible sunlight (280–750 nm), UV-A and visible sunlight (320–750 nm), and no sunlight. (Error bars represent standard error).

< 0.0001) and partial (Tukey simultaneous tests, $T = 6.612$, $P < 0.0001$) sunlight. There was no significant difference ($T = -0.815$, $P = 0.42$) in the number of *B. licheniformis* CFUs on cultures from feathers exposed to full-spectrum sunlight (280–750 nm) and those exposed to sunlight from which UV-B was blocked (320–750 nm).

DISCUSSION

The uninoculated control feathers exposed to full spectrum sunlight (280–750 nm), including UV-B radiation, were undamaged upon unaided visual inspection. Bergmann (1982) found that ultra-violet radiation damages feathers structurally, but the feathers he studied were exposed for a year or more on the backs of Lesser Black-backed Gulls (*Larus fuscus fuscus*). We found no differential damage (either macro- or microscopic) among the sets of feathers exposed under different conditions, even the inoculated feathers shielded from sunlight. This is not surprising, given that Cristol et al. (2005) reported no evidence of feather degradation by feather-degrading bacilli on the plumage of captive birds raised under semi-natural conditions. EHB has found that it may take as long as 4 months to see macroscopic damage on feathers exposed to *B. licheniformis* under simulated natural conditions. Our feathers were exposed for 5 weeks, which may not have been sufficient time to incur visible damage either from exposure to solar UV or through degradation by bacilli.

Most cells can repair DNA damage caused by UV radiation (5–400 nm) through either dark or light photo-reactivation repair mechanisms (Freidberg et al. 1995). During photoreactivation, the photo-reactivating enzyme (PRE) binds to the cyclobutane-type pyrimidine dimers formed by DNA irradiated with low wavelength UV (<320 nm; Sutherland 1981, Setlow 1995). This pyramidine-PRE complex is stable in the dark, but absorption of a photon in the wavelengths 350–500 nm breaks down the dimer into the constituent monomers and the PRE is released (Sutherland 1981). Other non photo-enzymatic processes such as excision, post-replication repair or dark repair can occur in the absence of light (Witkin 1976, Bauer 1998). UV-A radiation (320–400 nm) is the primary component of solar UV radiation reaching earth's surface

(Koller 1965), the higher wavelength component (350–400 nm) of which may facilitate photo-reactivation.

Inoculated feathers exposed to sunlight had significantly fewer feather-degrading bacilli than those not exposed to sunlight. The mean number of CFUs of bacilli were similar on feathers exposed to just UV-A and visible light, and those receiving UV-B, UV-A, and visible light (Fig. 2). However, although not statistically significant, the observed trend was consistent with the prediction that feathers receiving UV-B should have fewer bacilli (Fig. 2). This may be due to sustained repair of UV-damaged DNA in bacilli on feathers exposed to only UV-A and visible sunlight—initiated by dark or photo-reactivation and the absence of the especially harmful UV-B radiation. Exposure of inoculated feathers to sunlight with or without the potent UV-B wavelengths significantly reduced the presence of feather-degrading *B. licheniformis*, compared to those inoculated feathers shielded from sunlight.

Sunning seems to be one method by which feather-degrading *B. licheniformis* is controlled. Burtt and Ichida (1999) reported that incidence of feather-degrading bacilli on wild birds is lower during the summer when solar insolation is maximal than during late fall and winter. Muza et al. (2000) found that *B. licheniformis* occurs mainly on the outermost surface of the plumage, the distal portion of feathers, where spores or vegetative cells in the air and soil come in contact with the feather. Trapped in the distal structure of the feather, bacteria are exposed to sunlight, which makes it a likely agent for bacterial regulation. Unlike feather lice and mites (Moyer and Wagenbach 1995), bacteria are unable to seek refuge in the proximal portion of the feather. They are blocked by the dense network of barbules and are unable to degrade the distal portions of the feather rapidly enough to reach the proximal portions (Cristol et al. 2005). Muza et al.'s (2000) conclusion, the absence of feather damage in live birds despite inoculation with feather-degrading bacilli (Cristol et al. 2005), and the results of this study suggest the abundance of vegetative cells of feather-degrading bacilli on the feathers of birds would be higher and feathers would be more damaged were it not for avian maintenance behavior. Such behavior includes sunning, which renders the bacilli inactive by inducing spore-formation or killing them (Burtt and Ichida 1999, Cristol et al. 2005). We suggest that sunning, in addition to its other functions, may have evolved, in part, from strong selective pressure to regulate harmful plumage microflora such as feather-degrading *B. licheniformis*.

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PREDICTING POPULATION TRENDS OF THE BLACK-FACED SPOONBILL (*PLATALEA MINOR*)

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ABSTRACT.—The global population of the Black-faced Spoonbill (*Platalea minor*) has increased steadily. We estimated global population growth rates of the Black-faced Spoonbill based on annual counts of wintering populations in East Asia between 1991/1992 and 2003/2004. The mean (±SD) annual growth rate was 1.13 ± 0.08. The estimated survival rate was 86.6 ± 9.3% based on the annual return rates of color-banded birds in Taiwan between 1998 and 2005. We predicted global Black-faced Spoonbill populations in 2003/2004–2013/2014 using a stochastic exponential model and showed the mean global population in 2013/2014 would exceed 4,000 ± 950. The probability of a global population decline to less than the 2003/2004 level is low ($P = 0.06$). If the 1991–2004 growth rate is sustained, the probability for the global population to increase to twice that of the 2003/2004 level is 0.98 and the predicted mean wintering population in Taiwan could exceed 2,000 in 2013/2014. Establishment of new protective areas and increasing food availability at existing reserves and adjacent fish ponds in southwestern Taiwan will be necessary to ensure continued growth. *Received 9 September 2005. Accepted 24 July 2006.*

Knowledge of how a population changes over time can be used to forecast population size in the future. Population forecasts are important to conservation and management of threatened or endangered species. The Black-faced Spoonbill (*Platalea minor*) was classified by the IUCN and the Taiwan Government as "critically endangered" in 1992 (Hancock et al. 1992). The cause of the decline is unknown. But events, such as the Korean War (Collar et al. 2001), Vietnam War, Cultural Revolution in China, as well as wetland loss, environmental changes (Yeung et al. 2004), disease (Chyi and Hu 2003, Shiau et al. 2003), and poaching (Liu 2004) may have contributed to the decline of the Black-faced Spoonbill population. More attention has been focused on the species since 1992 (Severinghaus et al. 1995) and the global population of the Black-faced Spoonbill has increased steadily in the past decade. Only 288 birds were recorded in East Asia in 1988 (Kennerley 1990) but the population had increased to 1,206 individuals by winter 2003/2004 (Lee and Liu 2004).

Black-faced Spoonbills breed between April and September on islands along the coast of the Yellow Sea of the Korean Peninsula and China (Won 1966, Chong et al. 1996, Daimon 1997, Ueta et al. 2002, Kim 2004). In winter, Black-faced Spoonbills migrate to wintering sites along the coasts of Japan, Taiwan, the Philippines, Vietnam, Macao, Hong Kong, and China (Hachisuka and Udagawa 1951, Hancock et al. 1992, Lee et al. 1995, Mendoza et al. 2002, Ueta and Higuchi 2002, Ueta et al. 2002). Over 50% of the population in East Asia regularly overwinters in the coastal wetlands of southwestern Taiwan (Ueng and Kuo 1992; Dahmer and Felley 1996, 2000; Liu 2005). Since 1992, hunting of the birds was strictly prohibited and two wildlife reserves, the Chiku Black-faced Spoonbill Reserve and the Shihchu Wildlife Reserve, were established in southwestern Taiwan. The number of wintering birds in Taiwan has increased gradually since then.

We estimated the growth rate of global Black-faced Spoonbills based on existing data. We used the long-term data for Black-faced Spoonbills collected in southwestern Taiwan to analyze the proportion of the wintering subpopulation in Taiwan. We then used a stochastic exponential model (Akçakaya et al. 1999) to predict global population size and to estimate the size of the wintering Taiwan subpopulation in the next decade. We used the survival rate estimated from wintering birds in Taiwan, and the fecundity rate calculated from the above two parameters to predict global population size and the mean and variance of the global growth rates.

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METHODS

The Global Population.—The annual global population estimator of Black-faced Spoonbills between 1991/1992 and 2003/2004 was derived from the existing literature. We also estimated the annual global population size between 1991/1992 and 1996/1997 by summing winter count numbers (mainly Dec and Jan) in Japan, China, Hong Kong, Vietnam, and Taiwan (Scott and Rose 1989; Kennerley 1990; Perennou et al. 1990; Perennou and Mundkur 1991; Ueng and Kuo 1992; Dahmer and Felley 1994, 1995; S. Chan, pers. comm.). The annual global population size between 1996/1997 and 2003/2004 was estimated from synchronous counts of each wintering subpopulation in East Asia including South Korea, Japan, mainland China, Vietnam, Hong Kong, and Taiwan (Dahmer and Felley 2000, Lee and Liu 2004, Nguyen 2004).

The Taiwan Subpopulation.—The wintering population in southwestern Taiwan was counted from 1991/1992 through 2003/2004 in our study area on the coastal wetlands and fish ponds between the Yanshuei (23° 01′ N, 120° 08′ E) and Bajhang rivers (23° 20′ N, 120° 07′ E), encompassing a total area of 54 km^2. This study area included three main winter habitats of Black-faced Spoonbills: Chiku Lagoon (1,700 ha), Black-faced Spoonbill Reserve (300 ha), and the Shihchu Wildlife Reserve (522 ha). The number of Black-faced Spoonbills in Taiwan outside our study area was <5% of the entire Taiwan population (Liu 2005). Spoonbills were counted at least once per month from September to June each year. Results from an earlier survey in 1991/1992 indicated the wintering population size usually peaks in December (Ueng and Kuo 1992). Population surveys in December were therefore conducted at least twice per month (occasionally four times, weather permitting) in subsequent years. December surveys were usually made during cold fronts when Black-faced Spoonbills congregated in their primary habitats. During each daily survey, two observers traveled independently through established transects and counted birds perched on the ground. The monthly total was the high count during each month and the annual peak number was the maximum monthly count.

Statistical Analysis of the Growth Pattern.—The global population and Taiwan subpopulation trends from 1991/1992 to 2003/2004 were analyzed with linear regression from the logarithmic-transformed population size and time.

Estimation of Growth Rate.—Annual growth rates, $R(t)$, for the global population from 1991/1992 through 2003/2004 were calculated from annual counts where $R(t) = N(t + 1)/N(t)$, and $N(t)$ is the total number of spoonbills in year t. We also calculated the geometric mean and standard deviation of annual growth rates from 1991/1992 to 2003/2004.

Estimation of Survival Rate.—The survival rate of Black-faced Spoonbills was estimated based on data from 33 spoonbills color-banded in Taiwan between 1997 and 2003. Four, 12, and 17 birds were banded in the winters of 1997/1998, 1998/1999, and 2002/2003, respectively, at Chiku Wetland (Ueta et al. 2002, Yang et al. 2004). These banded birds were reobserved by Collin Chen and the authors between October 1998 and May 2005 in Taiwan (Ueta et al. 2002; Chen 2003; Collin Chen, pers. obs.). The annual survival rate was estimated from the return rate, which was the number of the reobserved birds in the wintering area in the current year divided by the number of reobserved birds in the previous year (Clarke and Kerry 1994). One banded bird was observed in Hong Kong in winter 2002/2003 and was included in the analysis.

Prediction of the Population Size in the Next Decade.—We used a stochastic exponential model (Akçakaya et al. 1999) with RAMAS EcoLab computer program (ver. 2.0, Sinauer Associates, Inc., Sunderland, MA, USA) to estimate global population sizes in the next 10 years (2003/2004–2013/2014). We used a fixed growth rate (R) defined as $N(t) = N(0)\cdot R^t$, where $N(t)$ and $N(0)$ are population sizes at years t and 0, respectively, for a deterministic exponential model. We allowed the annual growth rate, $R(t)$, to vary in the stochastic exponential model. The computer program generated a random number ranging from 0 to 1 to calculate the growth rate value from a cumulative percentage curve of the normal distribution of $R(t)$ for each predicted year. We used this sampled growth rate value and the estimated mean survival rate, s, to calculate the fecundity rate for the year [$f(t) =$

TABLE 1. Estimated global annual growth rates of Black-faced Spoonbill and counts of the subpopulation in southwestern Taiwan from 1991 to 2004.

	Global (East Asia)		Taiwan	
Year	Count[a]	Growth rate	Peak count	% Global
1991/1992	288		191	66
1992/1993	300	1.04	196	65
1993/1994	345	1.15	206	60
1994/1995	422	1.22	286	68
1995/1996	491	1.16	300	61
1996/1997	579	1.18	298	51
1997/1998	613	1.06	319	52
1998/1999	586	0.96	363	62
1999/2000	660	1.13	463	70
2000/2001	828	1.25	483	58
2001/2002	972	1.17	608	63
2002/2003	1069	1.10	705	66
2003/2004	1206	1.13	716	59
Mean ± SD		1.13 ± 0.08		62 ± 5
		1.11 ± 0.09[b]		

[a] 1991/1992–1995/1996 data from Ueng and Kuo (1992), Dahmer and Felley (1994, 1995), and S. Chan (pers. comm.). Data from 1996/1997 to 2003/2004 from Dahmer and Felley (2000), Lee and Liu (2004), and Nguyen (2004).

[b] Calculated from 1996/1997–2003/2004 data (synchronous counts).

$R(t) - s$]. Two computer-generated random numbers were assigned to each bird to ascertain its survival and reproductive success for the year. If the random number was greater than the survival rate, the bird died. If the random number was greater than the fecundity rate, the bird failed to produce offspring that year. This procedure simulated the demographic stochasticity. A time series (10 years) of the stochastic simulation for the population was considered a trial, which was replicated 1,000 times. The lowest and highest population sizes from each trial were used to construct an approximate decline (extinction) risk curve and an approximate increase (explosion) risk curve, respectively.

RESULTS

Growth Pattern of the Global Population.—Black-faced Spoonbills showed exponential growth from 1991/1992 to 2003/2004 (Table 1, Fig. 1). The geometric mean (± SD) of the annual global growth rates over the period was 1.13 ± 0.08, while the geometric mean based on only the rates calculated from the synchronous counts from 1996/1997 to 2003/2004 was 1.11 ± 0.09 (Table 1).

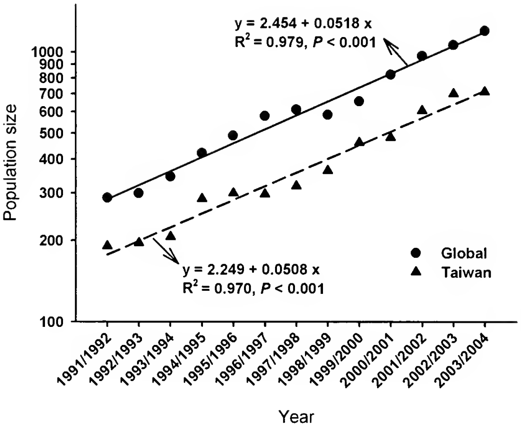

FIG. 1. Global population and Taiwan subpopulation size of Black-faced Spoonbills from 1991/1992 to 2003/2004. The population size on the Y-axis was logarithmic-transformed.

The Taiwan Subpopulation.—Monthly counts of wintering Black-faced Spoonbills from 1991/1992 to 2003/2004 peaked in December (Fig. 2). The wintering population in southwestern Taiwan ranged from 51.5% (1996/1997) to 70.2% (1999/2000) of the estimated global population (mean 61.7 ± 5.6%; Table 1). The Taiwan subpopulation (slope = 0.0508) closely tracked the global population (slope = 0.0518) from 1991/1992 to 2003/2004 (Fig. 1).

Survival Rate.—The annual survival (return) rates of banded Black-faced Spoonbills in Taiwan between 1998/1999 and 2004/2005 ranged from 0.75 to 1.0 (Table 2) with a mean annual return rate of 86.6 ± 9.3%.

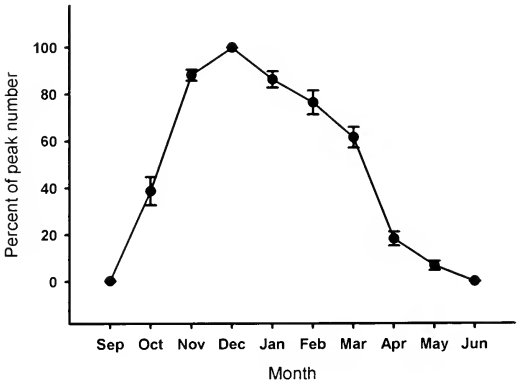

FIG. 2. Monthly changes in number of Black-faced Spoonbills wintering in Taiwan from 1991/1992 to 2003/2004. The peak number is the high count of the year. Symbols and error bars are means ±1 SE.

TABLE 2. Return rates of color-banded Black-faced Spoonbills between the 1998/1999 and 2004/2005 wintering seasons in southwestern Taiwan. Mean of return rates = 86.6 ± 9.3%.

		Number returned						
Year banded	*n*	1998–99	1999–00	2000–01	2001–02	2002–03	2003–04	2004–05
1997–98	4	3	3	3	2	2	1	1
1998–99	12		11	10	8	8	5	5
2002–03	17						16	13
Return rates		0.75	0.93	0.93	0.77	1.00	0.82	0.86

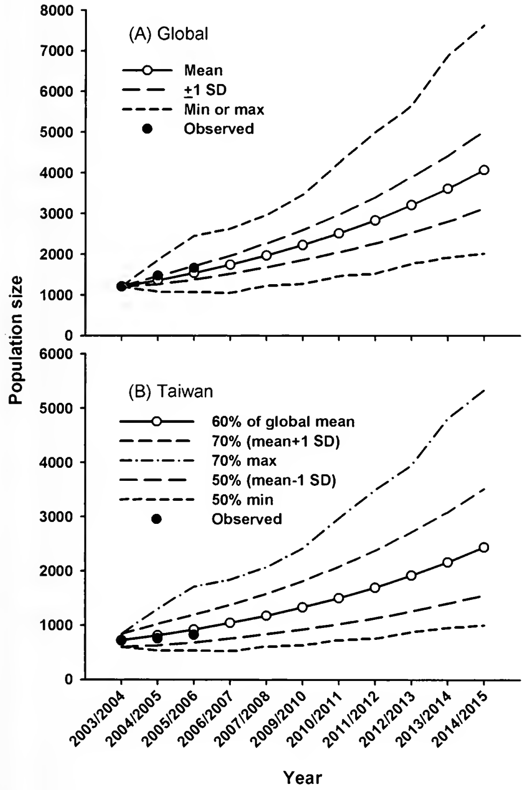

FIG. 3. Estimated population size of the Black-faced Spoonbill from 2003/2004 to 2013/2014. (A) Global trend estimated by a stochastic model with 1,000 simulations. Open circles and the long-dashed lines are means ± 1 SD. The short-dashed lines are minimums or maximums. (B) Taiwan subpopulation trend estimated from the global trend. The open circles are 60% of global means. The upper dashed line and the dash-dot line are 70% of global means +1 SD and 70% of global maximums, respectively. The lower long and short dashed lines are 50% of global means −1 SD and 50% of global minimums, respectively. The closed circles are the observed global or Taiwan population sizes.

Estimation of the Global Population for the Next Decade.—We estimate a mean global population in 2013/2014 of 4,066 ± 950 individuals with a minimum of 2,500 and a maximum of 7,500 individuals (Fig. 3A). This estimate was based on an initial population size of 1,206 (in 2003/2004) with a growth rate of 1.13 ± 0.08 and a survival rate of 0.87. The probability of the global population decreasing to less than the 2003/2004 level of 1,206 in next decade is approximately 0.06 (Fig. 4A), and the probabilities of the global population increasing to two or three times that of the 2003/2004 population are approximately 0.98 and 0.65, respectively (Fig. 4B).

Estimation of the Taiwan Subpopulation for the Next Decade.—Assuming Taiwan continues to support 60% of the global population, we estimate a Taiwan subpopulation in 2013/2014 of 2,450; this may vary from 1,560 (50% of global mean −1 SD) to 3,510 (70% of global mean +1 SD) (Fig. 3B). In rare scenarios, such as disease outbreaks or extreme weather conditions, it may range from about 1,200 (assuming a global minimum of 2,412 and Taiwan supporting 50% of the global population) to over 5,300 (assuming the global maximum of 7,615 and Taiwan supporting 70% of the global population) (Fig. 3B).

DISCUSSION

Sensitivity Analyses.—The growth rate had the greatest impact on predicted population size among the parameters used for the stochastic exponential model. The probability of the global population reaching 2,000 individuals is 1.0 (100%) if the mean growth rate is increased by 10% (R = 1.24). Conversely, if the mean growth rate is decreased by 10% (R = 1.02), the probability of the global population reaching 2,000 individuals decreases to 0.096 (9.6%) with an almost 90% difference

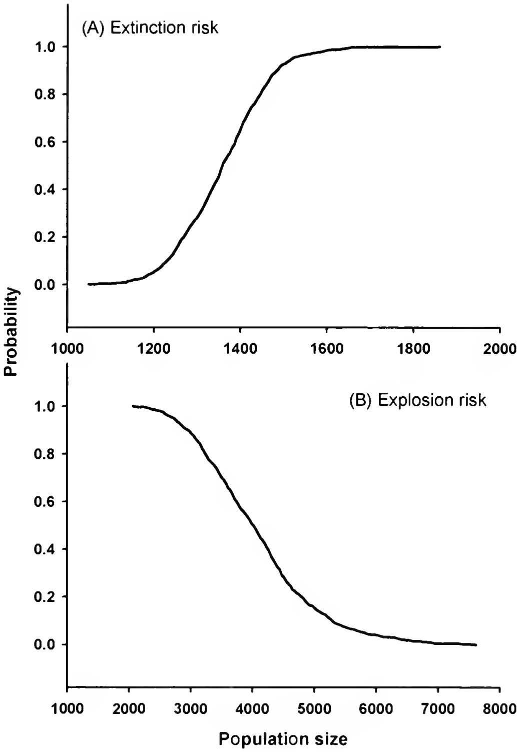

FIG. 4. Risk curves for the global Black-faced Spoonbill population from 2004/2005 to 2013/2014 based on a stochastic exponential model with 1,000 simulations. (A) Extinction risk curve and (B) explosion risk curve.

in probability. A similar change in the survival rate or in the standard deviation of the growth rate will result in a difference in the probability of <2.5%.

The annual growth rate, $R(t)$, was calculated as $N(t + 1)/N(t)$ which made it rather robust to sampling errors in field surveys. An overestimate of $N(t + 1)$ results in a large $R(t)$ and a small $R(t + 1)$ for the subsequent year and vice versa. However, sampling errors in surveys result in a larger standard deviation in $R(t)$. The fluctuation in the standard deviation of $R(t)$ has a relatively small impact on the predicted outcomes. The calculated mean growth rate (1.13) based on the 1991/1992–2003/2004 data differs from that based on synchronous counts (1.11) by less than 2% (Table 1).

The survival rate was estimated from the return rate of color-banded wintering birds and may overestimate the overall population survival rate since the return rate did not take into account first year birds. However, this overestimate probably would not significantly affect our predictions of the extinction/explosion probabilities, because they are not sensitive to change in survival rate. We consider the estimated return rate (86.6%) of wintering Black-faced Spoonbills reasonably accurate as it is similar to the return rate of adult Eurasian Spoonbills (*Platalea leucorodia*) (83%; Bauchau et al. 1998).

CONSERVATION IMPLICATIONS

Our results suggest the global population of Blacked-faced Spoonbills is not likely to decline and is most likely to double—and possibly triple in the next decade—if favorable conditions persist and the current trend continues. The trend of an increasing global population implies a need for additional or better winter habitats in Taiwan since 50–70% of the global population of Black-faced Spoonbills overwinter there.

Field surveys in 1999 led to the discovery of a new wintering subpopulation in Bajhang Estuary, 25 km north of the primary habitat (Chiku Lagoon). Prior to 2002/2003, only single digit numbers of Black-faced Spoonbills were recorded in Bajhang Estuary. The number of spoonbills there rapidly increased in January 2004/2005 and reached a peak of 63 birds in late March, when most of the birds at Chiku Lagoon had left the area (Dai and Chen 2005). At the same time, the number of the birds at Shihchu Wildlife Reserve, 8 km south of Chiku Lagoon, also reached a peak of more than 300 birds (Dai and Chen 2005). Coincidently, many fish ponds adjacent to the Chiku Lagoon were drained for sanitation after harvest, making it impossible for birds to feed. This strongly suggests that food for Black-faced Spoonbills in the Chiku Lagoon may be depleted in late winter causing the birds to move to other areas.

The need for protecting new habitats and for improving the food availability in existing habitats becomes apparent (Liang et al. 2002, Ueng et al. 2006) as the number of wintering birds increases. Maintaining fish ponds adjacent to suitable habitats and in good condition (i.e., shallow water with leftover fish) after harvest is also important and may be necessary. Support from the government is essential to increase the involvement of aquaculture farmers in the conservation of the spoonbill.

In addition to a food shortage, disease outbreaks, such as avian botulism that killed 73 Black-faced Spoonbills in winter 2002/2003 in Taiwan, can also threaten significant portions of the global population. Thus, it may be necessary to establish additional protected areas or reserves to reduce the risk of population decimation by disease.

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FIRST RECORDS OF WHITE-BROWED CRAKE (*PORZANA CINEREA*) FOR LAOS AND ITS CURRENT RANGE IN SOUTHEAST ASIA

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ABSTRACT.—All historical records of White-browed Crake (*Porzana cinerea*) in mainland Southeast Asia were south of the Isthmus of Kra, suggesting a Sundaic distribution. The first records from continental Thailand, Cambodia, Vietnam, and Laos revise the known resident distribution north almost to China. Information is inadequate to assess whether the species was historically overlooked across this huge area, or has genuinely expanded its range. Several factors suggest the latter, a pattern shown by no other bird species, and surprising given the pressing threats faced by wetlands and rallids in Southeast Asia. *Received 16 November 2005. Accepted 3 September 2006.*

The White-browed Crake (*Porzana cinerea*) inhabits well-vegetated lowland non-flowing wetlands from Southeast Asia east through New Guinea and Australia to Polynesia (Taylor 1996, 1998). Historical records in mainland Southeast Asia are from Malaysia, Singapore, and Thailand south of 8° N (Robinson and Chasen 1936) or "south of the Isthmus of Kra [~10° 30′ N]" (Deignan 1963). On 5, 8, and 11 March 2000, TDE (Robson 2000) discovered this crake (up to three birds) in Laos, at Nong Pen, Vientiane Municipality. JWD conducted 12 monthly boat-based surveys in this area in a 20-month period: December 2003; February, April through June, and August through November 2004; and January, March, and July 2005, and found the White-browed Crake to be resident. The species is distinctive and observations were often close, prolonged, and in good light. The diagnostic white supercilium was conspicuous even on birds seen only in flight, allowing many flushed birds to be identified. The objective of this paper is to describe observations at Nong Pen, Laos and discuss recent distributional records of the White-browed Crake in Southeast Asia.

OBSERVATIONS

Nong Pen (Fig. 1) expands greatly in area and depth during the wet season (May–Oct) from its dry-season area of ~500 ha. Its water surface is mostly vegetated with lotus (*Nelumbo nucifera*). Smaller-stemmed and -leaved species, commonly including the aquatic fern *Salvinia cucullata* and the dicotyledon *Ludwigia adscendens* (both native to Laos: Carlsson et al. 2004b) form thick floating mats. Two invasive exotics, water-hyacinth (*Eichhornia crassipes*) and water-lettuce (*Pistia stratiotes*), are not yet present; the former abounds in some Vientiane sites, the latter less so. In the shallower parts of Nong Pen are many beds of emergent grasses and sedges. Non-native giant mimosa (*Mimosa pigra*) infests much of the margin. Plant growth is rapid from May onwards, giving much of the lake a dense swampy nature, which lasts well into the dry season. In December, vegetation starts to die back, and heavy human collection of plant and animal material (for food), much from wooden canoe, destroys much of the macrophyte growth. By February 2004 there was little cover and in April 2004 and March 2005, there was none on the lake itself. The floating mats were thin and compacted, with no projecting stalks; the out-of-water lotus persisted only as many dead, leafless, stalks, and marginal vegetation was trampled and grazed by water buffaloes (*Bubalus bubalis*).

Each morning visit during 2003–2005 involved 2 hrs in a wooden canoe, specifically searching for skulking marsh birds such as rails. White-browed Crakes were seen in all months except April (3 Jan 2005, five birds; 16 Feb 2004, nine; 6 Mar 2005, one; 5 Apr 2004, zero; 14 May 2004, three; 7 Jun 2004, three; 8 Jul 2005, eight; 26 Aug 2004, five;

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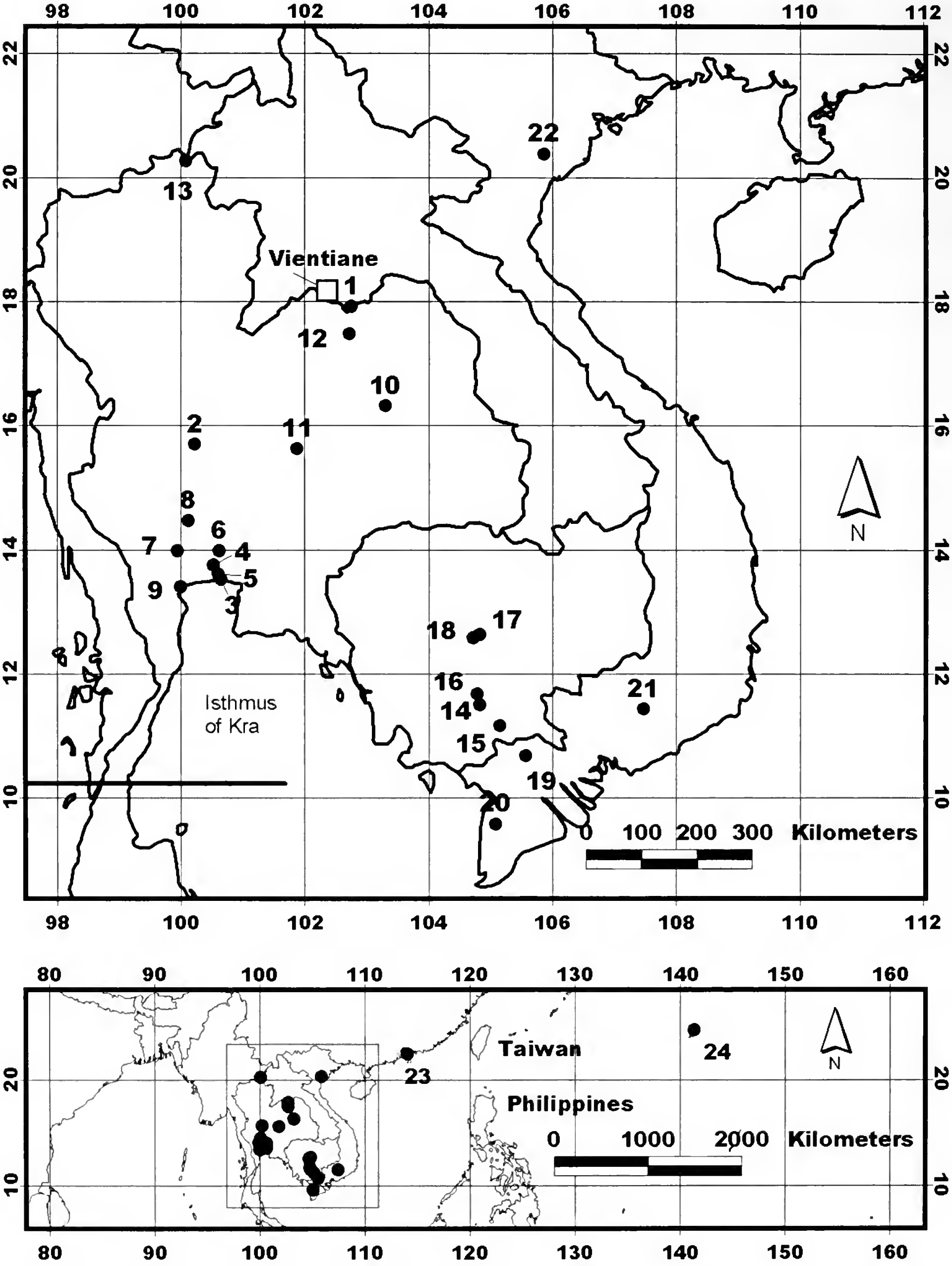

FIG. 1. Locality records of White-browed Crake from non-Sundaic mainland Asia. 1. Nong Pen (17° 55–56′ N, 102° 45′ E). 2. Bung Buraphet (15° 42′ N, 100° 14′ E). 3. Bang Pu (13° 31′ N, 100° 39′ E). 4. Nong Khaem (13° 45′ N, 100° 31′ E). 5. Khlong Bang Kaew (13° 22′ N, 100° 22′E). 6. Rangsit (13° 59′ N, 100° 37′ E). 7. Kamphaengsaen (13° 59′ N, 99° 57′ E). 8. Suphanburi (14° 28′ N, 100° 07′ E). 9. Samut Songkram (13° 24′ N, 100° 00′ E). 10. Bung Nong Bua (Maha Sarakham Province, 16° 19′ N, 103° 18′ E). 11. Nong Lahan (Chaiyaphum Province, 15° 38′ N, 101° 53′ E). 12. Nong Samrong (Udon Thani Province, 17° 28′ N, 102° 43′ E). 13. Nong Bong Khai (near Chiang Saen, 20° 16′ N, 100° 05′ E). 14. Unnamed site north of Phnom Penh (11° 30′ N, 104° 50′ E). 15. Bassac Marsh (11° 10′ N, 105° 09′ E). 16. Basset Marsh (also known as Lac Samroung; 11° 41′ N, 104° 47′ E). 17. Kruos Kraom (12° 38′ N, 104° 49′ E). 18. Veal Srangai (12° 35′ N, 104° 43′ E). 19. Tram Chim National Park (10° 41′ N, 105° 34′ E). 20. U Minh Thuong National Park (9° 35′ N, 105° 05′ E). 21. Cat Tien National Park (11° 26′ N, 107° 28′ E). 22. Van Long Nature Reserve (20° 23′ N, 105° 52′ E). 23. Mai Po (22° 30′ N, 114° 3′ E). 24. Volcano Islands (24° 47′ N, 141° 20′ E).

14 Sep 2004, two; 8 Oct 2004, one; 7 Dec 2003, three), although the sole bird seen in November (17 Nov 2004) could not be 100% certainly identified as this species. Most birds were foraging on floating *Salvinia* mats, close to concentrations of stems of *Nelumbo* and/or *Ludwigia*, presumably to allow easy access to cover. During the wet season, some birds were found clambering, apparently foraging, in the beds of monocotyledons and, at peak water-level, in flooded *Mimosa* stands. We made few observations from the shore, except for a static watch on 28 March 2005 to check for evening, especially vocal, activity by marsh skulkers; a White-browed Crake was seen to fly at dusk from the young rice in a wet paddy, to forage on an open floating mat. Paddies provided almost the only dense cover around the lake at that season; daytime retreat into them undoubtedly explains the low March and zero April counts from the boat. The low counts in September–November may reflect the large volume of habitat coupled with a post-breeding evasiveness typical in many birds. This hypothesis, however, needs to be confirmed by more rigorous quantitative survey (involving trapping to check for molt status).

DISCUSSION

The White-browed Crake has not been found in six other wetlands with dense semi-natural aquatic macrophytes around Vientiane city, which we visited during the same months as Nong Pen. Observations at these six sites were land-based, but the lengthy periods scanning superficially suitable vegetation, and this crake's general conspicuousness (Kennerley 1992; Taylor 1996; Wells 1999; JWD, pers. obs.), suggest it was effectively absent from those sites.

Nong Pen is ~800 km north of any historical mainland record. Laos's avifauna was poorly researched before 1990; surveys conducted during 1992–99 recorded 67 species new to the country (Duckworth 2006). The White-browed Crake may be one of the many species overlooked in Laos up to 1950, but our records are part of a pattern of massive expansion since 1980 of its known Southeast Asia range (Fig. 1). The White-browed Crake was found for the first time in central Laos on 3 March 2007 when at least four birds were observed in a lotus-dominated part of Nam Souy Lake, Savannakhet Province (16° 31′N, 105° 12′E (Dirk Van Gansberghe and Mathieu Baehrel, pers. comm.).

P. D. Round (pers. comm.) observed White-browed Crake in February 1983 at Bung Buraphet, Thailand, ~400–500 km north of where the species had been recorded previously in Thailand and only a few months after the first reports from Bung Buraphet. It occurs there year-round, many nests have been found, and it has since been found at many other Thai water bodies between Bung Buraphet and the Isthmus of Kra, including Bang Pu, around Bangkok (Nong Khaem), Khlong Bang Kaew, Rangsit, Kamphaengsaen, Suphanburi, and Samut Songkram (Ogle 1986, Round and Jukmongkol 2006b; Round and Gardner 2007). Its known range has recently been extended into northeast Thailand, at Bung Nong Bua, with two birds on 25 January 2004, in May 2004, and on 3 January 2005 (Nittaya Lawrence and R. A. Parks, pers. comm.; photographed), and one on 26 December 2004 (John Williamson, pers. comm.); at Nong Lahan on 20 February 2005 (Mark Mallalieu in Round and Jukmongkol 2005) and at Nong Samrong, where nine adults and three chicks were seen on 20 January 2006 (Round and Jukmongkol 2006c). This species has also been observed in north Thailand, with 7 birds at Nong Bong Khai over 19–23 December 2005, and 15 on 2 January 2006 (Round and Jukmongkol 2006a, 2006b).

The first records for Cambodia were in 1994, when Mundkur et al. (1995) recorded single crakes on 16 and 17 April at Bassac Marsh and an unnamed site north of Phnom Penh, respectively; on 1 May they photographed three of these crakes for sale at a Phnom Penh market. A single crake was seen on 26 January 1997 at Basset Marsh (Duckworth and Hedges 1998; JWD, pers. obs.). The White-browed Crake is now found regularly at both Basset and Bassac marshes, with counts peaking at 15 birds at the latter site (Goes and Poole 2002). Single birds were recorded from two other sites in Cambodia, both in the floodplain of the Great Lake of Tonle Sap in Kompong Thom Province: at Kruos Kraom daily during 18–21 January 2002 on a large lotus pond within deep-water rice-field and scrub mosaic, and at Veal Srangai on 6 April 2002 on a mud-fringed small pool within *Oryza* (wild rice) grassland (Peter Davidson, unpubl. data).

Buckton and Safford (2004) referred to the first record of the White-browed Crake from Vietnam: two separate incidents of single birds in photographs (by Nguyen Van Hung) of many crakes caught for food [mainly Baillon's Crakes (*P. pusilla*) and a few Ruddy-breasted Crakes (*P. fusca*)] taken near Tram Chim National Park during 1996–99 (S. T. Buckton, pers. comm.). Nguyen Phuc Bao Hoa (2004) listed the species from U Minh Thuong National Park as "rare" based on observations during April 1999 to March 2001. Nguyen Tran Vy et al. (2002) found 85 birds at Ta Lai and Da Bo around Cat Tien National Park in January–February 2002 (some birds were photographed), and Nguyen Tran Vy et al. (2003) found 162 birds at the same sites in January–February 2003. The birds were in floating-grass mats, moving into wet rice paddies to find food. The previous status in these parts of Cat Tien is difficult to assess because, before 2002, the floating-grass mats were not checked and the rise in counted numbers by 2003 may merely reflect that playback of tape-recorded calls specifically for the species was used in that year. Playback at many other sites in the Park in 2003 did not find the species (Nguyen Tran Vy, pers. comm.). However, single White-browed Crakes were found at Crocodile Lake (within Cat Tien National Park) in January 2004 (S. C. P. Doppagne, pers. comm.) and on 22 March 2004 (P. W. Logtmeijer, pers. comm.), and two were found there on 11 February 2005 (S. C. P. Doppagne, pers. comm.). Crocodile Lake was frequented by birdwatchers in the 1990s, but the species was apparently not seen in that interval (Gert Polet, pers. comm.).

Van Long Nature Reserve recently provided an "amazing range extension" (Robson 2004) into northern Vietnam. S. C. P. Doppagne (pers. comm.) saw 1 bird at this site on 13 December 2003, 2 on 22 February and 5 December 2004, at least 14 on 16 January 2005, 3 or 4 on 17 July 2005, and 1 adult with 3 newly-hatched chicks on 6 August 2005. A. W. Tordoff (pers. comm.) also found an adult and at least two juveniles on 13 August 2005. The species is clearly resident at Van Long, as it is at Nong Pen.

A single White-browed Crake occurred during 20–28 April 1991 in Hong Kong at Mai Po (Kennerley 1992, Carey et al. 2001). However, we have traced no records from mainland China.

The White-browed Crake is widespread in the Philippines (Dickinson et al. 1991) and has occurred on islands farther north, with six records from Taiwan between April and November (Wang et al. 1991; "Bird Database of Wild Bird Federation Taiwan" provided by Woei-Horng Fang, pers. comm.). This crake inhabited the Volcano Islands of extreme southern Japan until the early twentieth century (Ornithological Society of Japan 2000).

The Sundaic (Thai-Malay Peninsula, Borneo, Java, Sumatra, and associated islands) avifauna is distinct from that further north in southeastern Asia; many Sundaic species' northern range limits lie on the peninsula around the Isthmus of Kra (Round et al. 2003). The White-browed Crake's known mainland range since 1980 has expanded from a purely Sundaic distribution north almost to China. It is not clear whether this 'expansion' is the result of genuine range change, recent detections of the species where historically it was overlooked, or both. Previous coverage of the "new" sites was too minimal for the lack of historical records to be interpreted as confirming the crake's absence at any one of them. P. D. Round (pers. comm.) considers it could have been previously overlooked even at well-covered Chiang Saen, Thailand. The species' history at Cat Tien is consistent with recent colonization, but might simply reflect site-specific habitat succession. Thus, the evident trend cannot be extrapolated to the wider region.

The lack of a single historical record north of the Isthmus of Kra, the broad distribution of recent records, the multiple records from small and degraded sites close to large cities, and the species' rather conspicuous behavior all indicate genuine range expansion. As a group, if small marsh birds had been under-surveyed historically in non-Sundaic Southeast Asia, other resident species should surely also have been found in areas far from their previously known range. No other bird species has extended its known distribution from the Isthmus of Kra almost to China, at least not in the last half-century. However, without good data on wetland characteristics through time, it is not possible to identify causes behind changes in range. Wells (1999) considered the White-browed Crake on the Thai-Malay peninsula "mostly dependant" on transient, man-made habitats. The wetlands with the recent new records are also artificial or heavily modified. Other regional changes, either known or inferred, that may or may not be affecting the crake's distribution include major shifts in plant, fish, and aquatic invertebrate communities with introductions and range expansions of non-native species, eutrophication, expansion of wet rice cultivation in the dry-season and, conceivably, shifts in climate.

CONSERVATION IMPLICATIONS

Despite the suggested expansion of the White-browed Crake's range, Indochinese wetlands face severe threats. They continue to be lost through conversion to paddies and dry land habitats (e.g., Claridge 1996; Round and Gardner 2007). Wetland birds are hunted assiduously, especially in Laos. During our surveys, hunting methods observed included snares set amid dense vegetation and at the water's edge, shooting, catapulting, aerial lines of hooks, and mist-netting. Duckworth et al. (1999) listed most marshland bird species that were bigger than *Ixobrychus* bitterns as "At Risk in Laos" or "Potentially At Risk in Laos"; our survey fully supports those listings. Other than the White-browed Crake, the Common Moorhen (*Gallinula chloropus*) was the only rallid regularly found at Nong Pen. The moorhen and White-breasted Waterhen (*Amaurornis phoenicurus*) are the only rallids recently recorded both frequently and widely in Laos (Duckworth et al. 1999). That the White-browed Crake might greatly have expanded its geographic range is not a positive indication of overall marsh bird status in Indochina.

A new threat to the White-browed Crake is the South American golden apple snail (*Pomacea canaliculata*). This snail at high densities can almost eradicate aquatic macrophytes, resulting in their replacement by planktonic algae (Carlsson et al. 2004a, Carlsson and Lacoursière 2005). Villagers reported to Carlsson et al. (2004b) that both *Salvinia cucullata* and *Ludwigia adscendens* (plants used extensively by foraging crakes, and, largely, forming the floating mat substrate) "disappeared from the Vientiane wetlands since the snail was introduced". *Pomacea* has already colonized Nong Pen, but it is unclear whether the snail and aquatic macrophytes successfully coexist there, or whether the snail is simply a new colonist; it arrived in Laos as recently as 1991 (Duangboupha et al. 2002). Nong Pen is not well-connected to other wetlands (as demonstrated by the lack of water-hyacinth there), and our subjective assessment indicated much lower densities of snail-egg masses at Nong Pen than at some other surveyed wetlands of Vientiane.

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Short Communications

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Similarities Between *Campephilus* Woodpecker Double Raps and Mechanical Sounds Produced by Duck Flocks

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ABSTRACT.—The search for the Ivory-billed Woodpecker (*Campephilus principalis*) in eastern Arkansas and northwestern Florida has yielded double raps recorded by autonomous recording units (ARUs) in White River National Wildlife Refuge and along the Choctawhatchee River, respectively. These double raps have been presented as suggestive evidence for the presence of the species in those regions. We present data comparing double raps produced by wing collisions from an aerial Gadwall (*Anas strepera*) flock to double raps documented by ARUs. Close similarities in amplitude ratios, peak-to-peak times between raps, and auditory quality between ARU recordings and wing collisions from a Gadwall flock illustrate the ability of flying ducks to produce sounds easily mistaken for the double raps of *Campephilus* woodpeckers. All ARU double raps suggesting the presence of an Ivory-billed Woodpecker should be reconsidered in light of the phenomenon of duck wingtip collisions, especially those recorded during winter months when duck flocks are common across flooded bottomlands of the southeastern United States. *Received 25 January 2007. Accepted 28 February 2007.*

Evidence for survival of Ivory-billed Woodpeckers (*Campephilus principalis*) in Arkansas and Florida includes recordings of "double raps" (DRs) from autonomous recording units (ARUs) in White River National Wildlife Refuge (WRNWR) and along the Choctawhatchee River, which sound much like the double raps of some *Campephilus* woodpeckers (Charif et al. 2005, Hill et al. 2006). Although no unequivocal recording of the double rap of an Ivory-billed Woodpecker (IBWO) exists, written descriptions indicate it was similar to those of other members of the same genus (Tanner 1942). We believe many ARU DRs from Arkansas and Florida were likely produced by aerial duck flocks when flock members flying in close proximity hit wingtips. We observed three sets of DRs produced by flying Gadwall (*Anas strepera*) flocks at WRNWR on 21 December 2005. Prior to this observation, we were unaware of the "duck wingtip collision" (DWC) phenomenon, and we subsequently discussed our finding with members of the 2005–06 Cornell Laboratory of Ornithology search crew. We then observed and recorded an identical event from a Gadwall flock at Eagle Lake, Texas on 2 January 2006. In both cases, these sounds were associated visually with duck flocks. No visual sightings were associated with ARU recordings. CDJ worked as a member of the IBWO search team from December 2004 to April 2005. During this time, to his knowledge, field crews were not informed of the DWC phenomenon. Here we compare DWCs from our recording with ARU DRs from 24 January and 5 February 2005 (http://www.birds.cornell.edu/ivory/multimedia/sounds).

METHODS

We recorded a series of DWCs from a Gadwall flock using a Sony TCM5000EV cassette recorder with a Sennheiser MKH416T shotgun microphone at Eagle Lake, Texas (96° 19′ 43″ W, 29° 35′ 15″ N) on 2 January 2006. We measured times between rap peaks and peak-to-peak amplitude ratios for two Eagle Lake DWCs, and three ARU DRs from 24 January and 5 February 2005 (Table 1). In addition we made similar measurements for DR recordings of four *Campephilus* species: Pale-billed Woodpecker (*C. guatemalensis*), Powerful Woodpecker (*C. pollens*), Robust Woodpecker (*C. robustus*) (audio S3 in Charif et al. 2005), and Red-necked Woodpecker (*C. rubricollis*) recorded by LYP in Peru in November 2005 (Table 1). We produced a low-volume recording from the *C. rubricollis* re-

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TABLE 1. Peak-to-peak times and amplitude ratios for five double rap recordings (two DWCs and three ARU DRs), with ranges for four *Campephilus* woodpeckers; Pale-billed (*C. guatemalensis*), Powerful (*C. pollens*), Robust (*C. robustus*), and Red-necked Woodpecker (*C. rubricollis*).

Recording	Peak-to-peak time (ms)	Amplitude ratio
Eagle Lake A	65	1.78
Eagle Lake B	108	1.36
ARU January	102	2.76
ARU February A	84	0.79
ARU February B	75	3.72
Campephilus	57–82	0.73–1.00

cording for equitable comparison with the distant Eagle Lake recording (Fig. 1). We calculated peak-to-peak amplitude ratios by dividing the peak amplitude of the second rap by that of the first, for each DR. Times between raps were calculated by subtracting the time of peak amplitude occurrence of the first rap from that of the second. All audio spectrogram measurements were made using program Raven (Charif et al. 2004).

RESULTS

Two DWCs from the Eagle Lake recording were of sufficient quality for analysis (http://www.talltimbers.org/research/duckraps.htm). Additional DWCs were audible in the recording, but measurements were inconclusive due to background noise and distance from the flock. We analyzed only the second ARU DR from the 24 January 2005 recording and the second and third from the 5 February 2005 recording, as the other raps were too faint for conclusive measurement.

Peak-to-peak rap times and amplitude ratios of ARU DRs from 24 January and 5 February 2005 were similar to those of DWCs recorded at Eagle Lake, Texas. Peak-to-peak rap times for ARU DRs and DWCs were either similar to or slower than examples from *Campephilus* species (Table 1). Amplitude ratios for two ARU DRs and both DWCs were greater than those measured for these *Campephilus* species (Table 1). The peak-to-peak time and amplitude ratio ranges shown (Table 1) for these extant *Campephilus* species do not represent full ranges of possible values, but are intended

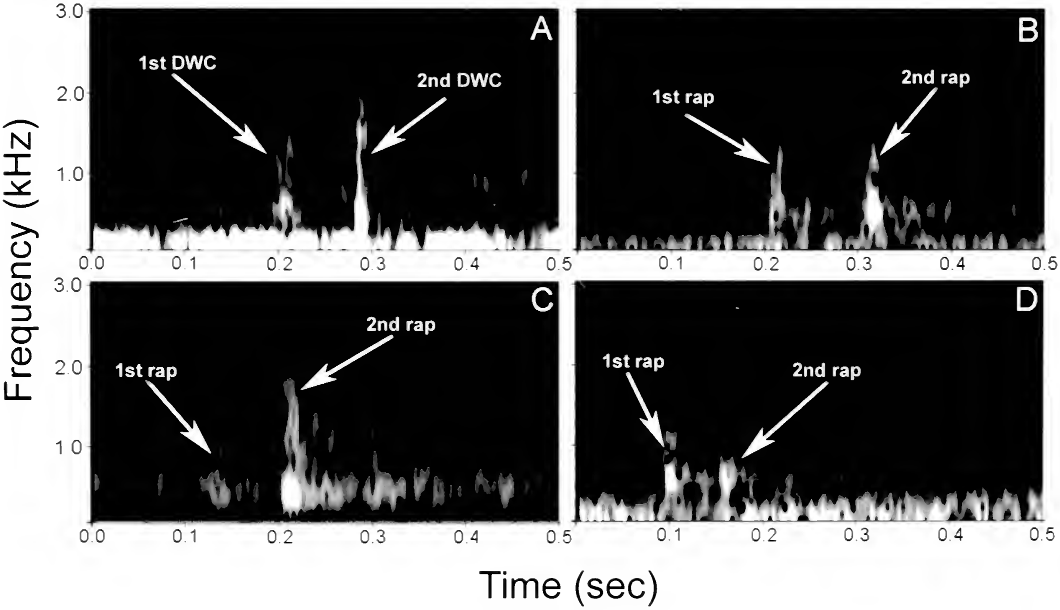

FIG. 1. Audio spectrograms of (A) duck wing collisions from Eagle Lake, Texas, (B) ARU recording 24 January 2005, (C) ARU recording 5 February 2005, and (D) low volume *C. rubricollis* double rap to simulate distance and quality of Eagle Lake recording. Color value is proportional to power in decibels (e.g., black represents lowest power, white represents highest power). Amplitude (not shown) of second rap is greater than amplitude of first rap in panels A, B, and C. Amplitude of first rap is greater than second in panel D.

to represent ranges within which typical *Campephilus* DRs would be expected to fall. These comparisons illustrate the ease with which DWCs could be mistaken for *Campephilus* DRs.

DISCUSSION

Two ARU DRs from Arkansas and both DWCs consisted of a second rap greater in amplitude than the first, strengthening the possibility that these and other such ARU raps were produced by ducks and, more importantly, decreasing the likelihood the sounds were produced by Ivory-billed Woodpeckers. While Tanner (1942) described the typical DR of *C. principalis* as a louder first rap followed by a softer second rap, other *Campephilus* species are known to occasionally produce DRs with a second rap louder than the first. However, these are considered atypical; such DRs occurred in only 18% of a sample of 119 DRs recorded from seven *Campephilus* species (Fitzpatrick et al. 2006). Only 45% of 99 DRs recorded from Choctawhatchee River fit the description of Tanner (Hill et al. 2006). Therefore, DWCs provide a more plausible explanation for the source of ARU DRs than do multiple recordings of atypical *Campephilus* DRs.

The second DR from the February ARU recording appears to fit Tanner's description. However, all DRs from this recording show a particularly strong likelihood of being DWCs, as they are accompanied by audible wing sounds produced by flying ducks and a Gadwall vocalization. This suggests that DWCs may even account for some ARU DRs in which the first rap is greater in amplitude than the second; considerable variability in the amplitude and spacing of the two raps in such random events as duck wingtip collisions is to be expected.

Our suspicion that many ARU DRs were produced by ducks is further reinforced by the similarity in auditory quality between the ARU and Eagle Lake recordings, in contrast to the acoustic quality of other *Campephilus* recordings (audio S3, audio S4 in Charif et al. 2005). *Campephilus* drums on a wooden substrate typically consist of a crisp tone followed by brief reverberation, whereas our DWCs and publicly available ARU DRs consist of dull tones lacking reverberation.

Campephilus species typically produce a series of DRs from a single perch that are delivered at fairly regular intervals over periods of many minutes. However, all available ARU DR recordings from WRNWR (http://www.birds.cornell.edu/ivory/multimedia/sounds) have been short events consisting of only a few DRs. Of those recordings, one contains only a single DR event. The remaining two each contain only three DRs recorded in very short time periods, the longer of the two lasting approximately 42 sec. From the Choctawhatchee River, 69 of 99 recorded DRs were singletons (Hill et al. 2006), and the remaining 30 are present in recordings containing between two and nine DRs. A recording containing repeated double raps spaced fairly evenly over a period of many minutes, rather than brief events lasting only a short time, would constitute more plausible acoustic evidence for the presence of an Ivory-billed Woodpecker than any current putative recordings that are publicly available.

The occurrence of a distant DR followed by a closer, louder DR in the WRNWR ARU recordings has suggested to some that they were call-and-response interactions between at least two Ivory-billed Woodpeckers (Charif et al. 2005). An extremely similar event occurs in our Eagle Lake recording. However, these DWCs were produced by a Gadwall flock flying away from the recording unit, with the second DWC more distant than the first. DRs present in the January ARU recording were likely produced by a duck flock flying toward the ARU, with the first DR more distant than the second.

A treatment of the DWC phenomenon, incorporating our observations but without additional confirmed recordings, was given in the Cornell Laboratory of Ornithology's 2005–06 final report (Rohrbaugh et al. 2006), where the number of plausible ARU DRs was concurrently reduced from hundreds to 10. The temporal distribution of those DRs is highest during the winter months and declines in abundance in the spring months. This pattern accords well with a migratory winter duck population, but the reduced use of ARUs in the spring months could easily account for the apparent correlation (see Table 6, Rohrbaugh et al. 2006). A more detailed account of the specific dates of recordings would help elucidate this potential relationship and the ARU DRs accumulated in Florida should be given a similar treatment. Additional ARU efforts, if undertaken, should be extended to summer months when migratory ducks are largely absent from the southeastern United States, but resident woodpeckers would be expected to remain territorially active.

Charif et al. (2005) and Rohrbaugh et al. (2006) acknowledged that DRs recorded by ARUs do not confirm the presence of Ivory-billed Woodpeckers in Arkansas. However, until this time no other North American bird (or other sound source) was known to consistently produce *Campephilus*-like DRs, making Ivory-billed Woodpeckers seem the most likely candidates. Before any ARU DR is considered to be even suggestive of the presence of an Ivory-billed Woodpecker in a region where duck flocks are common, it should be conclusively shown the sound was not produced by duck wingtip collisions.

Considering WRNWR hosts a large wintering duck population, wingtip collisions produced by flying ducks provide an alternative explanation for the source of ARU DRs and must be considered as the search for the Ivory-billed Woodpecker continues. Any DRs delivered in series and recorded during the summer, when wintering duck flocks are absent from the southeastern United States, would merit especially careful analysis.

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Breeding Behavior of the Chihuahuan Raven

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ABSTRACT.—The Chihuahuan Raven (*Corvus cryptoleucus*) is abundant and conspicuous throughout its range, but much remains unknown about its breeding biology and social system. We studied the breeding biology of this species in southern New Mexico in 2000 and 2001, and hypothesized that environmental variability of desert habitats represents a major selective force. We predicted that variable food supplies and limited nest sites might select for cooperative provisioning of young similar to behavior in several other members of the genus *Corvus*. We examined nesting behavior and social relationships of nesting groups. Nest observations revealed that both males and females incubate eggs, brood nestlings, and feed young. Nesting pairs were primarily territorial in the immediate vicinity of the nest, but occasionally tolerated intruders, and at other times were joined by the intruders in communal mobbing of potential predators. Average group size near the nest was 1.7 birds and we did not detect auxiliary birds at or near the nest. We found no sign of cooperative breeding in the population of Chihuahuan Ravens we studied. However, we did find cooperation in predator defense within groups of nesting ravens. *Received 7 April 2005. Accepted 8 October 2006.*

Chihuahuan Ravens (*Corvus cryptoleucus*) are generally restricted to arid habitats of southwestern United States and north central Mexico (Bednarz and Raitt 2002). They are common and abundant in their range, yet much of their basic life history remains unknown or poorly documented, particularly in regard to social relationships and territoriality during the breeding season.

Among the seven North American species of *Corvus*, two exhibit cooperative breeding: the eastern and western subspecies of the American Crow (*C. brachyrhynchos*) (Chamberlain-Auger et al. 1990, Verbeek and Caffrey 2002), and the Northwestern Crow (*C. caurinus*) (Verbeek and Butler 1981). The Common Raven (*C. corax*) is a solitary breeder, with no reports of colonial nesting or cooperative breeding (Goodwin 1986, Heinrich et al. 1994). The possibility of cooperative behavior has been reported for the Chihuahuan Raven, although the true status remains unclear (Heinsohn et al. 1990). Aldous (1942) observed a breeding pair and nonbreeding individuals giving alarm calls in the vicinity of a single occupied nest, and Jollie (1976) reported communal nesting, but gave few details.

We examined nesting behavior and composition of breeding groups over two breeding seasons. We hypothesized that environmental variability of desert habitats represents a major selective force on the breeding biology of Chihuahuan Ravens that may favor development of cooperative breeding (Ligon 1999, Ligon and Burt 2004). Given the variable environment, helpers might increase opportunities for adequate provisioning of young, particularly when conditions are poor. Unpredictable and harsh environmental conditions typical of Chihuahuan Raven breeding habitat may cause helpers to choose to help when the costs of rearing young outweigh the benefits (Emlen 1982).

METHODS

The study area (32° 10′ N, 106° 55′ W) was approximately 78 km^2 (perimeter = 37 km) on a mesa adjacent to the Rio Grande River Valley, 11–19 km southwest of Las Cruces, New Mexico. The land is managed by the Bureau of Land Management and was grazed heavily by cattle between the 1930s and 1970s, and moderately thereafter (L. J. Bevacqua, pers. comm.). The predominant plant species in this desert scrub habitat included honey mesquite (*Prosopis glandulosa*), soaptree yucca (*Yucca elata*), fourwing saltbush (*Atriplex canescens*), longleaf ephedra (*Ephe-*

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dra trifurca), snakeweed (*Gutierrezia* spp.), and peppergrass (*Lepidium* spp.).

We captured Chihuahuan Ravens using a cage-trap (Aldous 1936) and a rocket-net (model S200, Winn-Star, Inc., Marion, IL, USA) between February and July, 2000 and 2001. We marked ravens with federal leg bands, and one or more of the following: colored leg bands, patagial tags, bleached feathers, and radio transmitters. The patagial tags were of rip-stop nylon fabric of either a solid color or striped and attached to the patagium with size 3 Jiffy wing tags (National Band and Tag Company, Newport, KY, USA). Wing or tail feathers of some birds were bleached in unique patterns using BW2 Clairol Professional Powder Lightener and Brentwood Salon Care Crème Developer. We used two-stage and one-stage radio transmitters, weighing 16–19 g (<3.8% of raven's body mass) and 9–12 g (<2.4% body mass), respectively, attached to a harness of Teflon ribbon. Subsequently, we monitored territories and noted marked adults. We marked nestlings in 2000 with unique patagial tags to examine site fidelity between years and if they were helpers or breeders as yearlings. We took blood samples from the brachial wing vein to identify the gender of marked birds. We used a commercial firm (Avian Biotech International, 1336 Timberlane Road, Tallahassee, FL, USA) for gender analysis using dot-blot DNA assays (Ellegren 1996, Griffiths et al. 1998).

We systematically searched the study area for raven nests from a vehicle, ATV, and on foot from February through June, 2000 and 2001. Egg laying generally begins in May and continues into early June (Bednarz and Raitt 2002). Nests were usually 3–5 m above ground level in mesquite trees. Ravens often reuse nests from previous years; therefore, old nests are most easily detected in February and March when mesquite trees are without leaves. During late spring into summer, nests are somewhat hidden by foliage, but still easy to detect from a distance as a large, dark clump in a tree. We checked each nest for signs of use with a mirror pole every 10 days after discovery. All nests presumed to be in use were checked with a mirror pole once every 3 days to ascertain nesting stage and contents. We recorded the number of ravens within 500 m of the nest and noted their activities.

We observed each nest for up to 60 min prior to checking for nest contents to assess territorial behavior. Observations were from a distance ≥500 m to minimize disturbance to the ravens while allowing good visibility of activities. We recorded the number of ravens within visible range (~1,000 m), their individual behaviors, and duration of each activity during nest observations. Activities monitored included nest attendance, nest defense, social interactions, and feeding.

RESULTS

We marked 112 adult Chihuahuan Ravens in 2000 and 11 in 2001. The patagial tags and radio transmitters worked best for identifying individuals from a distance. Colored leg bands were of limited value because we were unable to get sufficiently close to see them without disturbing the birds. Bleaching of feathers required handling ravens for 20 min or more, did not produce as many unique patterns as other marking methods, and bleached feathers were not easily observed from a distance. We equipped 11 birds with radio transmitters during February–June 2000 and detected five within the study area during the breeding season; four of these bred that year. The six remaining birds likely left the study area as they were not observed subsequently. Two adults marked with patagial tags in 2000 used the same nest in both years. Another adult marked with a patagial tag in 2001 also bred that year. In 2000, we marked 28 nestlings on 14 territories with patagial tags to examine their breeding status in 2001. We saw two yearling ravens in the study area in 2001 that had been marked as nestlings in 2000. We found no indication that either was breeding.

We did not detect more than two ravens attending a nest during 222 hrs of nest monitoring in 2000 (n = 23 nests) and 2001 (n = 25 nests). However, at times we found only one bird in attendance because ravens often left the nesting area, presumably to feed. Mean (± SD) length of nest observations was 10.9 ± 4.3 min (n = 1,120 observation sessions). Although our goal was to conduct hour long observations, this was seldom possible because the birds often detected us long before the period was over and, once detected, we left the area. The mean (± SD) number of observations for each nest was 23.3 ± 10.4 (n = 1,120). The variation resulted from differences in the length of the monitoring period for each nest (mean = 61 ± 23.7 days, n = 48 nests) which was influenced by the stage when the nest was first located and if it was successful.

We estimated territory size based on nest density to quantify territorial behavior. Mean (± SD) distance between nests was 656 ± 304 m (n = 34) and minimum distance between nests was 207 m. We considered territories to include an area equivalent to a circle centered on the nest with a radius equal to the minimum distance (207 m) between nests. We restricted analysis of territory observations to that area. Number of adults present simultaneously (group size) on territories averaged 1.7 ± 0.03 birds (n = 784 observations of 44 nests) and was rarely more than two individuals. We saw additional ravens on territories on 65 occasions (8.3%). On 42 of those occasions (65%), these "extra" birds were tolerated by the nesting pairs. They were either ignored or, at times, joined in flight by one or both member(s) of the nesting pairs. At no time were the "extra" birds at or near the nesting tree. In the 23 remaining instances, "extra" ravens either clearly were chased by the nesting pairs (4 occasions) or they joined with the nesting pair in giving alarm calls (19 occasions) and aggressive displays as they mobbed a nearby predator [i.e., Swainson's Hawk (*Buteo swainsoni*), Northern Harrier (*Circus cyaneus*), or coyote (*Canis latrans*)]. In seven instances, the extra birds were known to come from neighboring territories; in the other instances it was not clear from where the birds originated.

In both years, four (17% in 2000, 16% in 2001) of the monitored nests had at least one marked breeder. We ascertained gender for three of these based on blood samples taken when the birds were captured for marking. Behavioral observations revealed that both males and females incubate eggs, brood nestlings, and feed young. We observed nine nest exchanges between adults at five nests during observations totaling 170 min. One nest exchange occurred during the early egg stage and the remaining eight when the nestlings were between 4 and 20 days of age. Between nest exchanges, individual adults incubated or brooded between 1 and 65 min, averaging 14 min (±18.4, n = 14). On five occasions, we found males in active nests (n = 2). On one occasion during the nestling stage (5–7 days of age), a male was in its nest for a total of 65 min. Parents fed young during 27 nest observations (n = 387). In eight (30%) cases, both parents were present and participated in the feedings; at times one adult fed the second adult (gender unknown) and both adults then fed the nestlings.

DISCUSSION

In cooperatively breeding birds, helpers are often yearlings (Brown 1987, Skutch 1999) as is the case with crows (Caccamise et al. 1997, Caffrey 2000). In 222 hrs of nest observations of 48 different nests, we did not observe ravens other than members of breeding pairs participate in any form of helping behavior such as incubation of eggs, brooding of young, or feeding of adults or young. We did not have any evidence of ravens other than the nesting pair at or in the immediate vicinity of a nest. Group size on territories over two seasons gave no indication of the presence of helpers on the territory (mean group size = 1.7 birds). In two separate studies of the American Crow, the presence of auxiliary birds was clearly indicated by the mean group sizes on territories of 4.4 and 2.9 birds (Chamberlain-Auger et al. 1990, Caccamise et al. 1997, respectively). We compared group size on Chihuahuan Raven territories with similar group size observations for crows (Caccamise et al. 1997). The occurrence of group sizes greater than two was significantly (χ^2_2 = 471.4; $P < 0.001$) less frequent for ravens (8.3% observations) than for crows (59.2%).

We marked nestlings in 2000 with the intent of recognizing families the following year. Our 96 hrs of observation within the study area in 2001 detected only two of 28 nestlings marked in 2000. Neither showed any signs of helping or breeding, rather they were seen in the vicinity of a windmill within the study area that serves as an important water source and common gathering site for groups of ravens throughout the year. Most nests appeared to be tended by a male and female pair only. We found no evidence for cooperative breeding in this population of Chihuahuan Ravens.

Territorial defense by Chihuahuan Ravens occurs primarily in the immediate vicinity of the nest where they defend territories against conspecifics and other species. Extra birds are tolerated at times by nesting pairs at the periphery of territories. This was most common when nesting birds joined with others to participate in predator defense. We did not observe extra birds near the nest (<25 m) without eliciting a defensive response from the nesting pair. Nests often were well within view of one or more other nests. The practice of nesting in groups with neighboring nests well within auditory and visual range may facilitate the group defense behavior we observed.

Chihuahuan Ravens are socially active during both breeding and nonbreeding seasons and, unlike Common Ravens (Heinrich et al. 1994), they appear to form loose social units. In the population we studied, social groups were not obvious during the breeding season because adults were dispersed across breeding territories. However, when a predator approached a territory and the resident birds reacted defensively, a general group response of all nearby ravens was often elicited. This behavior may be the basis for the original observation of breeding and nonbreeding birds giving alarm calls near a nest (Aldous 1942) that led to speculation of cooperative breeding in Chihuahuan Ravens (Jollie 1976). However, we detected no sign of cooperative breeding in the population of Chihuahuan Ravens we studied. We did find cooperation in predator defense within groups of nesting ravens.

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Diet of Black and Turkey Vultures in a Forested Landscape

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ABSTRACT.—Black (*Coragyps atratus*) and Turkey (*Cathartes aura*) vultures feed heavily on carrion from domestic animals in agricultural landscapes. A recent study indicates vultures at a forested site in South Carolina had much larger home ranges than those residing in agricultural landscapes. Vulture home ranges at the forested site contained few residential or agricultural lands, and we hypothesized that vultures at that site fed extensively on wild carrion. We collected 65 regurgitated pellets from a communal night roost between 16 October 2000 and 9 April 2002 to test this hypothesis. The pellets contained undigested parts of consumed carrion including hair, bone, scales, and claws. Wild mammals, particularly white-tailed deer (*Odocoileus virginianus*), common raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and striped skunks (*Mephitis mephitis*), were common food items. The only domestic animal recovered (in two pellets) was the house cat (*Felis catus*). This study supports the observations that carrion resources affect distributions and movement patterns of Black and Turkey vultures. *Received 15 August 2005. Accepted 28 July 2006.*

Black (*Coragyps atratus*) and Turkey (*Cathartes aura*) vultures feed heavily on carrion from domestic animals in landscapes dominated by agriculture (Yahner et al. 1986, Coleman and Fraser 1987, Prior 1990, Yahner et al. 1990, Hiraldo et al. 1991). However, few data are available concerning diets of vultures in primarily non-agricultural landscapes (Thomaides et al. 1989). The available evidence suggests that diets of these scavengers vary across their geographic ranges (Thomaides et al. 1989, Prior 1990, Yahner et al. 1990, Hiraldo et al. 1991) and across seasons (Yahner et al. 1986, Coleman and Fraser 1987). DeVault et al. (2004b) observed vulture home ranges at the Savannah River Site (SRS) in South Carolina were essentially twice the size of those reported from an agricultural area in southern Pennsylvania and northern Maryland (Coleman and Fraser 1989). Home ranges at the SRS contained little residential or agricultural land, and DeVault et al. (2004b) hypothesized that vultures at SRS had to travel greater distances to find carrion and fed primarily on wild carrion.

An understanding of vulture diet composition and movement patterns is of critical importance to the aviation industry because Black and Turkey vultures are among the species most likely to collide with military aircraft operating at low altitudes (DeVault et al. 2005). Vultures are considered to be second only to deer in risk posed to civil aviation with 67% of collisions resulting in damage to the aircraft (Dolbeer et al. 2000). Telemetry evidence suggests that availability and distribution of carrion are important factors affecting vulture movement, and may influence the potential for catastrophic collisions with aircraft (DeVault et al. 2005). The objective of our study was to describe diets of Black and Turkey vultures roosting at SRS and to relate their diets to vulture movement patterns (DeVault et al. 2004b, 2005).

METHODS

Study Site.—The SRS is a 78,000-ha limited access nuclear production and research facility owned and operated by the U.S. Department of Energy on the Savannah River near Aiken, South Carolina. Approximately 64% of SRS is managed as commercial pine (*Pinus* spp.) plantations by the U.S. Forest Service with an additional 15% of the land classified as bottomland hardwood (Workman and McLeod 1990). Several industrial areas occur throughout the site and there are no agricultural or residential areas within the site boundary.

Collection of Pellets.—Vultures regurgitate indigestible portions of their meals (i.e., hair, bone, and feathers) as pellets (Kirk and Moss-

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man 1998, Buckley 1999). We collected 65 fresh pellets (ranging from 8–16 pellets/trip) between 16 October 2000 and 9 April 2002 from a communal night roost for hundreds of Black and Turkey vultures on the roof of the R-Reactor, an abandoned nuclear reactor. We initially planned to collect samples at regular intervals (i.e., quarterly) during a 2-year period but, because of security concerns, we were only able to make six trips to one portion of the reactor's roof. Observations during the trips suggested that ~70% of the vultures present were Black Vultures. Thus, our sample likely included pellets from both species.

Identification of Samples.—We treated each pellet as a separate sample. Upon collection, each pellet was placed into a plastic bag, sealed, and transported to Indiana State University. Pellets were soaked overnight in sealed jars to loosen the material and dissected in a glass Petri dish for analysis. Hair identifications were made using a combination of published keys (Mathiak 1938, Williams 1938, Mayer 1952, Stains 1958, Cotheran et al. 1991) and direct comparisons with specimens in the vertebrate collections at Indiana State University, Purdue University, and the Indiana State Museum. Feathers, bones, claws, and skin fragments were compared directly to samples obtained from museum collections and local farms. Initial, coarse identifications were made using physical characteristics of hairs under a 10–35× zoom dissecting microscope (Stains 1958). Identifications were verified by comparing individual hairs to known samples using a 40–1,000× binocular comparison microscope.

We report the frequency of food items and a modified estimate of average percent volume. Percent volume has been criticized (Coleman and Fraser 1987) because not all food items are equally digestible. However, we see no reason this argument should apply to fine keratinized structures. Thus, we removed large structures (bones, claws, teeth) and non-animal material from the Petri dish and visually estimated the percent hair, feathers, and scales belonging to each taxa for each pellet. Some species were only detected from larger remnants, but the value of using modified percent volume is that it provided an important tool in distinguishing major food items from those that are frequently, but incidentally ingested (i.e., vulture down).

TABLE 1. Food items of Black and Turkey vultures from the Savannah River Site in South Carolina.

Taxa	Frequency (%)	Volume (%) ($\bar{x}$ ± SD)
Metazoa	98	
Insecta (Formicidae)	2	
Reptilia (Colubridae)	2	Trace
Aves	34	4 ± 13
Cathartidae	34	4 ± 13
Meleagris gallipavo	2	
Mammalia	98	96 ± 14
Odocoileus virginianus	42	30 ± 44
Procyon lotor	37	32 ± 45
Didelphis virginiana	18	17 ± 37
Mephitis mephitis	15	13 ± 33
Felis catus	3	2 ± 13
Scalopus aquaticus	2	0
Sciurus niger	2	2 ± 13
Sylvilagus floridanus	2	1 ± 6
Plantae	85	
Poaceae	37	
Unknown	29	
Quercus leaves	15	
Thatch	3	
Juniperus virginiana	2	
Leaf litter	2	
Unidentified twig	2	
Unidentified seeds	2	
Non-biological material	11	
Soil	6	
Plastic	6	
Polystyrene	2	
Paper bag	2	

RESULTS

Wild mammals, particularly white-tailed deer (*Odocoileus virginianus*, 42% frequency), common raccoons (*Procyon lotor*, 37%), Virginia opossums (*Didelphis virginiana*, 18%), and striped skunks (*Mephitis mephitis*, 15%), were common food items (Table 1). The only domestic/feral animal recovered was the house cat (*Felis catus*), recovered from two pellets. Other mammals present in the diet included eastern mole (*Scalopus aquaticus*, 2%), fox squirrel (*Sciurus niger*, 2%), and eastern cottontail (*Sylvilagus floridanus*, 2%). Non-mammalian prey was rare, but some pellets included Wild Turkey (*Meleagris gallipavo*, 2%), a snake (cf. Family Colubridae, 2%), and ants (Formicidae, 2%). Vulture down (34%) was found in many pellets, but because it occurred in low percent volumes (mean = 4%), we suspect it was ingested during preening. Plant material (85% frequency) composed a minor portion of the volume of most pellets. Some anthropogenic materials were present, including plastic, paper bags, and polystyrene.

DISCUSSION

Vultures at SRS fed almost exclusively on wild carrion in our study. Feral cats are known to occur at SRS (Cotheran et al. 1991) and were likely the source of hair recovered from two pellets. Previous studies in both agricultural and relatively pristine landscapes (Paterson 1984, Yahner et al. 1986, Coleman and Fraser 1987, Thomaides et al. 1989, Prior 1990, Yahner et al. 1990, Hiraldo et al. 1991) suggested that insectivores and rodents would constitute an important component of the diets. However, the only small mammal in the pellets was a young (based on skeletal morphology) eastern mole (*Scalopus aquaticus*). Black and Turkey vultures at SRS were photographed feeding on mouse-sized carcasses experimentally placed throughout SRS during the same time period (DeVault et al. 2004a). Thus, we were surprised that small mammals were not a common component of the diet.

Three observations led us to suspect most of the carrion consumed by vultures during this study was obtained from road-killed animals. First, the diet of these vultures was dominated by medium-to-large-sized mammals (98% frequency, 96% volume), which were commonly observed dead along the roads (T. L. DeVault, unpubl. data). Second, 37% of the pellets contained grass and the only grass we could identify was Bermudagrass (*Cynodon dactylon*), which is commonly planted along roadways at SRS. Vegetation consistent with scavenging in woodlands (oak leaves and leaf litter) was present in only 17% of the pellets. Woodland vegetation is adjacent to roadways in this heavily forested landscape. Third, anthropogenic materials (plastic sandwich bags, brown paper sacks, and polystyrene) were present in several pellets; we suspect this represents road-side trash. Our data provides little insight into the presettlement diets of vultures in the study area as they relied heavily on road-killed animals for food.

Causes of animal mortality and by extension, type, amount, and availability of carrion resources available to vultures and other scavengers, vary widely across regions (DeVault et al. 2003). Our study suggests that diets (i.e., wild animals) of vultures at SRS differ markedly from those in agricultural regions in southern Pennsylvania and northern Maryland where domestic animals dominate the diet (Coleman and Fraser 1987). Black and Turkey vultures apparently can adjust foraging behaviors to best exploit available carrion resources. This adaptability has most likely contributed to recent range expansions of both species into the northeastern United States (Rabenold 1989). Future human-induced alterations to availability and type of carrion resources accessible to vultures (caused either by changes in land use, agricultural practices, or by increases in road kill) likely will continue to influence vulture distributions in the United States and elsewhere.

Type and availability of carrion at a local scale can also influence movement patterns of individual vultures. For example, vultures at SRS exhibited much larger home ranges (DeVault et al. 2004b) and flew more often and at higher altitudes (DeVault et al. 2005) than vultures in agricultural regions in southern Pennsylvania and northern Maryland (Coleman and Fraser 1989). Continued development of bird avoidance strategies by aircraft operators (e.g., Lovell and Dolbeer 1999) should consider how the amount and availability of carrion resources contributes to differences in vulture flight behaviors among regions (DeVault et al. 2005). Similarly, managers whose goal is control vulture populations must understand the potential of their activities to change the behaviors of individual vultures. Future inter-regional studies of vulture ecology (e.g., roost dynamics) should provide a better overall understanding of vulture biology and, ultimately, improved management strategies for vultures.

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Incidence of Nest Material Kleptoparasitism Involving Cerulean Warblers

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ABSTRACT.—We document 21 observations of interspecific stealing of nesting material involving Cerulean Warblers (*Dendroica cerulea*), Red-eyed Vireos (*Vireo olivaceus*), Blue-gray Gnatcatchers (*Polioptila caerulea*), Northern Parulas (*Parula americana*), Black-throated Green Warblers (*D. virens*), American Redstarts (*Setophaga ruticilla*), and Orchard Orioles (*Icterus spurius*) that occurred during studies of Cerulean Warbler breeding biology. These incidents involved a variety of combinations of nest owner and nest material thief suggesting that each of these species is both a perpetrator and recipient of this behavior in our study areas. Kleptoparasitic incidents occurred at all stages of the nesting cycle from nest-building through post-fledging. Two possible motivations for this behavior are related to saving time in finding nest materials and collecting this material for nest construction. *Received 21 November 2005. Accepted 3 September 2006.*

The Cerulean Warbler (*Dendroica cerulea*) is a canopy-nesting bird of eastern deciduous forests. Nests of this species are composed mainly of bark fiber, fine grass stems, weed stalks, hairs, spider webs, grapevine bark, lichen, and moss (e.g., Bent 1953, Ehrlich et al. 1988, Oliarnyk and Robertson 1996, Hamel 2000). Nests are typically on horizontal branches and are concealed from above by nest-tree and/or vine foliage (Bent 1953, Hamel 2000, Roth 2004). Few published studies have documented interspecific nest kleptoparasitism involving Cerulean Warblers. Hamel (2000) noted in the Mississippi Alluvial Valley that Cerulean Warblers and American Redstarts (*Setophaga ruticilla*), and Cerulean Warblers and Blue-gray Gnatcatchers (*Polioptila caerulea*) interacted aggressively over nesting materials. Cerulean Warblers have also been observed gathering nesting materials from vireo nests (species unspecified) in New Jersey (Dater 1951).

Cerulean Warbler breeding biology studies have focused on nest observation beginning in 1992 in Tennessee and Arkansas, and in 2002 in southern Indiana. This paper documents 21 interspecific contests for nesting material involving Cerulean Warblers that were observed during stages of the nesting cycle (Table 1). We present three detailed accounts of nest material kleptoparasitism involving Cerulean Warblers as both victim and perpetrator. Owner defense usually started at the point at which the owner discovered the robber at its nest.

OBSERVATIONS

The following two accounts document nest material kleptoparasitism with the Cerulean Warbler as victim. The first incident occurred on 19 May 2003 between 1230 and 1300 hrs CST when a Red-eyed Vireo (*Vireo olivaceus*) was observed taking material from a Cerulean Warbler nest in a grove of black walnut (*Juglans nigra*) at Big Oaks National Wildlife Refuge (39° 03′ N, 85° 25′ W) near Madison, Indiana. The vireo landed on the nest branch within a meter of the nest, then flew to the nest and removed a piece of the outer cup when the Cerulean Warbler was not present. The nest material was sufficiently large to be seen in the vireo's beak as it flew to a more densely wooded area. No bird visited the nest for a period of several minutes until a vireo again landed on the nest branch. The vireo hopped toward the nest when the male Cerulean Warbler chased it into the heavily wooded area. The female Cerulean Warbler then flew to the nest and sat in it. The female Cerulean Warbler was first observed building the nest on 8 May and incubating on 17 May. She was last observed incubating on 29 May and the nest had failed on 31 May. The walnut

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TABLE 1. Nest material kleptoparasitism involving Cerulean Warblers recorded during Cerulean Warbler breeding biology studies in Tennessee, Arkansas, New York, and Indiana.

Study area	Date	Nest owner	Stage	Kleptoparasite
Meeman Shelby Forest, TN	9 May 93	Cerulean Warbler	Building	American Redstart
Meeman Shelby Forest, TN	15 May 93	Cerulean Warbler	Building	American Redstart
Meeman Shelby Forest, TN	16 May 93	Cerulean Warbler	Abandoned	American Redstart
Meeman Shelby Forest, TN	23 May 97	Cerulean Warbler	Building	American Redstart
Meeman Shelby Forest, TN	24 May 97	Cerulean Warbler	Building	American Redstart
Chickasaw NWR, TN	7 Jun 93	Cerulean Warbler	Building	Blue-gray Gnatcatcher
Chickasaw NWR, TN	22 May 94	Cerulean Warbler	Incubation	Blue-gray Gnatcatcher
Chickasaw NWR, TN	23 May 94	Cerulean Warbler	Immediately after depredation	Blue-gray Gnatcatcher
Chickasaw NWR, TN	5 Jun 94	Cerulean Warbler	Abandoned	Blue-gray Gnatcatcher
Desha, AR	11 May 93	Cerulean Warbler	Abandoned	Blue-gray Gnatcatcher
Desha, AR	13 May 93	Cerulean Warbler	Dismantling and Cerulean Warbler reconstructing	Blue-gray Gnatcatcher
Desha, AR	28 May 93	Cerulean Warbler	Dismantling and Cerulean Warbler reconstructing	Blue-gray Gnatcatcher
Meeman Shelby Forest, TN	10 Jun 93	Cerulean Warbler	Incubation	Blue-gray Gnatcatcher
Yellowwood State Forest, IN	29 May 05	Cerulean Warbler	Building	Black-throated Green Warbler
Meeman Shelby Forest, TN	11 May 94	Cerulean Warbler	Building	Northern Parula
Desha, AR	14 May 93	Cerulean Warbler	Incubation	Orchard Oriole
Desha, AR	27 Jul 93	Cerulean Warbler	Unknown	Orchard Oriole
Big Oaks NWR, IN	19 May 03	Cerulean Warbler	Incubation	Red-eyed Vireo
Ulster County, NY (Smith 2001)	26 May 99	Red-eyed Vireo	Abandoned	Cerulean Warbler
Hoosier National Forest, IN	6 May 05	Red-eyed Vireo	Building	Cerulean Warbler
Meeman Shelby Forest, TN	11 May 93	Blue-gray Gnatcatcher	Immediately after depredation	Cerulean Warbler

grove had an open canopy, permitting detailed observations of the birds' behavior.

The second incident occurred on 29 May 2005 between 1030 and 1130 hrs when a female Black-throated Green Warbler (*Dendroica virens*) was observed taking material from a Cerulean Warbler nest in Yellowwood State Forest (39° 12′ N, 86° 21′ W) near Bloomington, Indiana. It landed on the nest branch within 1 m of the nest, approached it in a quick hopping manner, and stole nest material. The female Black-throated Green Warbler repeated this behavior three times and each time she was chased from the nest by the female Cerulean Warbler. In one of the three incidents, a male Cerulean Warbler was observed chasing with the female Cerulean Warbler. Eventually, both male and female Cerulean Warblers exhibited aggressive behavior (making repeated harsh call notes and chasing) toward the female Black-throated Green Warbler any time she perched within 15 m of the nest. The male Black-throated Green Warbler was not observed participating in chasing or nest robbing. The Cerulean Warbler nest was in a red elm (*Ulmus rubra*) near a planting of shortleaf (*Pinus echinata*) and eastern white pine (*P. strobus*). This may have increased the chances of proximity to a Black-throated Green Warbler territory, as that species is often associated with coniferous forests (Morse 1993).

The following account describes nest material kleptoparasitism with Cerulean Warbler as the perpetrator. On 6 May 2005 between 1430 and 1500 hrs a female Cerulean Warbler was observed taking material from a Red-eyed Vireo nest in the Pleasant Run Unit of the Hoosier National Forest (39° 01′ N, 86° 20′ W) near Bloomington, Indiana. The Cerulean Warbler made three separate trips from its own nest to the vireo nest approximately 30 m to the east, each time successfully acquiring material. On the first trip, the vireo presumably did not detect the Cerulean Warbler, as no interaction occurred; however, the vireo gave chase on the warbler's second and third trips. The stolen material was sufficiently large to be seen in the Cerulean Warbler's beak, and was incorporated into its nest. Both the Cerulean Warbler and the Red-eyed Vireo nests appeared to be mostly completed at the time of the raid. Construction of the Cerulean Warbler nest was first observed on 4 May 2005 at 1230 hrs; on 26 May 2005 the nest was confirmed to have failed.

DISCUSSION

The studies in which these observations occurred were specifically focused on Cerulean Warbler nests and it is not surprising that most incidents (18 of 21 observations, Table 1) involved Cerulean Warblers as victims rather than perpetrators. Most observations of female Cerulean Warblers returning to their nests with nesting material did not include observing them collect the material. Therefore, Cerulean Warblers may be robbing other nests more often than we are aware.

Red-eyed Vireos and Black-throated Green Warblers are not unlikely participants for nest material thievery interactions with Cerulean Warblers. Red-eyed Vireos are one of the most abundant bird species in our study areas (KCJ and KLR, pers. obs.), and both Red-eyed Vireos and Black-throated Green Warblers forage at the same heights where Cerulean Warbler nests occur (Morse 1993, Cimprich et al. 2000). Additionally, and perhaps most importantly, Cerulean Warblers, Red-eyed Vireos, and Black-throated Green Warblers may have similar requirements for nest composition and compete for materials. Red-eyed Vireos have been documented to use all of the same materials as Cerulean Warblers, with the exception of moss, in their nests (Harrison 1975, Ehrlich et al. 1988, Cimprich et al. 2000). Black-throated Green Warblers have been documented to use all materials except grapevine bark and lichen (Ehrlich et al. 1988, Morse 1993).

Prolonged completion of nest building may indicate that nest robbing has taken place, as was likely the case in the second nest robbing account. In this case, the Cerulean Warbler nest was probably not the pair's first attempt of the season based on the late date of nest construction. They began building their second nest on 25 May 2005, four days before nest robbing was observed. Immediately prior to observing nest material kleptoparasitism, the female Cerulean Warbler was seen bringing nesting material to her nest. As replacement nests are typically constructed more quickly than first nests, a 5-day spread of nest building was unexpected (KCJ and KLR, pers. obs.). Despite the interference, the nest successfully fledged at least two offspring.

Why would individuals risk physical conflict with neighboring birds to steal nesting material? It is possible that (1) some materials may take a great amount of time to locate, and (2) some materials may not be difficult to locate, but may be difficult to remove and collect in quantity in an appropriate size or shape to be incorporated into a nest (Yezerinac 1993).

Nest material may be in limited supply, as a result of the large demand for it by a variety of users, or the phenology of the source is limited in time. Nest construction is a time-consuming process, as it requires the adult bird to locate materials, to gather the materials into the nest site, and to form the actual nest. Nest construction appears to be a costly process in terms of energy expenditure. This process involves a multitude of flights to gather material. Bent (1953) indicated a single female American Redstart might make 700 trips in the construction of a single nest. The female pulls material from sources, such as dried cambium of broken tree branches and grapevines, even from inner portions of stems of herbaceous materials. The female must identity the most useful adhesive materials for attaching nests to supports and for holding surfaces together. "Spider webs" or silk from cocoons of emerged moths are often listed as the adhesive material. A variety of types of spider silk exist; variation among species may indicate that some may be more useful than others and the possibility of discriminate selection by avian users (Gosline et al. 1999, Žurovec and Sehnal 2002). Early nesting behavior may in part be favored by the ability to find the most effective nest materials. Competition for materials that are limited in time may occur between users of the favored material, irrespective of cost considerations.

Benefits of stealing nest materials are substantial reductions in (1) distance the female must travel from her nest, (2) time spent away from her nest, and/or (3) amount of effort spent while away from the nest. Birds may be more likely to resort to time-saving nest kleptoparasitism because the benefits outweigh the risks. The Red-eyed Vireo and the Black-throated Green Warbler may have robbed Cerulean Warbler nests because of the pressure of time during what was probably (based on the time of season) their second nesting attempt.

Another potential benefit of engaging in nest kleptoparasitism is decreased predation risk. Nest building birds may experience increased predation risk when gathering so much material in such a short period of time, often from relatively few locations which are repeatedly visited. Canopy-nesting species must often resort to gathering nesting material near or on the ground. These sites are not typical for the species; the birds may have less experience with the potential escape routes from predators available in such situations. The large number of sorties to and from a nest site increases the likelihood that a nest parasite may observe the location, follow the progress of the construction, and time their parasitic laying event. It is equally possible that other species, including but not limited to birds, mammals, snakes, and parasitic insects, may also observe locations frequented by nest building birds. Banks and Martin (2001) noted that when visitations by nest owner decreased in frequency, rates of Brown-headed Cowbird (*Molothrus ater*) nest parasitism increased. Therefore, less time spent foraging for nesting materials would allow the female more time for activities such as egg-laying and nest guarding.

All of these factors, acting individually or in concert, indicate that time of nest construction is a critical part of the life cycle of a bird, when the most important reproductive activities, including mate selection and egg production, occur. Study of the process is difficult, particularly for small species that nest in tree canopies in forest habitats. It is difficult to observe canopy-nesting species gathering nesting materials. Consequently, few data exist on predation risks associated with gathering nest material and the propensity to avoid certain locations as sites for gathering material.

It is not clear exactly how advantageous or disadvantageous kleptoparasitism of nest material is to individuals which participate in it. The perpetrators in all three detailed accounts presented, consistently returned to the victimized nests, despite the threat of being chased, indicating the rewards of kleptoparasitism outweighed the risks. One of the two Cerulean Warbler nests that was raided was successful. This indicates that victimization did not necessitate failure. The Cerulean Warbler pair that stole from the vireo nest was unsuccessful in raising young despite any benefits obtained from nest robbing. Further studies on nest robbing behavior, as related to the phenology, availability, and selection of nest materials will contribute to our understanding of when a nest-building female engages in nest material kleptoparasitism.

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Home Range and Dispersal of Juvenile Florida Burrowing Owls

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ABSTRACT.—We present the first use of necklace radio transmitters to document the home range and dispersal of juvenile Burrowing Owls (*Athene cunicularia floridana*) during the breeding and post-breeding period in rural Florida. Juvenile Burrowing Owls ($n = 4$) were detected close to main and satellite burrows during 65 day-time relocations. Home range estimates (95% kernel) for juvenile owls varied from 98 to 177 m^2. Juvenile Burrowing Owls were not detected near main and satellite burrows during three evening relocations. Dispersal of juvenile owls coincided with flooding of burrows during the rainy season. Juvenile owls upon fledging used an extensive patch of saw palmetto (*Serenoa repens*) before dispersing beyond the range of ground telemetry capabilities. Aerial telemetry assisted in locating one juvenile Burrowing Owl using scrub oak (*Quercus* spp.) habitat approximately 10.1 km southeast of its main and satellite burrows. *Received 16 February 2006. Accepted 7 October 2006.*

Early observations of Florida Burrowing Owls (*Athene cunicularia floridana*) describe their propensity to excavate burrows in short grass habitat (Hoxie 1889, Rhoads 1892, Scott 1892, Palmer 1896). Typically, a breeding pair of owls excavate one breeding burrow and one or more satellite burrows (Scott 1892, Neill 1954, Wesemann 1986, Mealey 1997). Burrows, which can be 1–3 m in length, contain an enlarged nest chamber at their terminus (Rhoads 1892, Scott 1892, Nicholson 1954, Sprunt 1954). Male and female Florida Burrowing Owls can breed at 1 year of age (Haug

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et al. 1993) with most females laying eggs in the spring (Nicholson 1954, Courser 1976, Millsap and Bear 1990). However, nesting can occur between October and July with 2–10 eggs/nest (Rhoads 1892, Scott 1892, Nicholson 1954, Owre 1978, Stevenson and Anderson 1994). Previous ecological research on Florida Burrowing Owls has occurred during the breeding period in urban areas including college campuses (Courser 1976), private residences (Mealey 1997), and vacant lots (Wesemann 1986; Millsap and Bear 1990, 1997, 2000).

The majority of ecological data on Florida Burrowing Owls in rural areas is observational and was collected in the late nineteenth and early twentieth centuries on dry prairie habitat in southcentral Florida (Ridgway 1874, Cahoon 1885, Hoxie 1889, Rhoads 1892, Scott 1892, Palmer 1896, Bent 1938, Nicholson 1954). There are no published studies from rural areas (agricultural lands, grazing land for cattle, and areas managed or maintained as natural habitat) in Florida that document productivity, survival, prey preference, dispersal, or habitat requirements (breeding and post-breeding) of Burrowing Owls.

Identifying habitat requirements for Florida Burrowing Owls in rural areas is particularly important because of the rate of habitat loss due to development. Florida's human population is the third fastest growing in the nation (U.S. Department of Census 2004) and a variety of habitats is being lost such as upland forests (Sprott and Mazzotti 2001), scrub oak (Myers 1990), and prairie habitats (Abrahamson and Hartnett 1990). There are no management strategies for Burrowing Owls in rural environments (Florida Fish and Wildlife Conservation Commission 2004a).

The objectives of our study were to estimate home range size and dispersal of juvenile Burrowing Owls in a rural environment. We also estimated size of home range of juvenile Burrowing Owls during the breeding season, measures of dispersal from breeding habitat, and the location and type of post-breeding habitat occupied by juvenile Burrowing Owls.

METHODS

The study was undertaken from 1 March to 5 August 2004 on Rutland Ranch, Bradenton, Florida (27° 30′ N, 82° 15′ W). Rutland Ranch encompasses 2,372 ha and is managed by the Southwest Florida Water Management District (Barnwell et al. 2003). The ranch contains a mixture of habitats including oak scrub, herbaceous marshes, riparian hardwoods containing laurel (*Quercus laurifolia*) and water oak (*Q. nigra*), pine flatwoods containing slash pine (*Pinus elliottii*) and saw palmetto (*Serenoa repens*), and non-native pastures. Burrowing Owls excavate burrows within a 81-ha rectangular portion of improved pasture that undergoes yearly prescribed burning. The major land uses surrounding Rutland Ranch include cattle ranching and agriculture.

We captured and fitted radio transmitters to seven juvenile Burrowing Owls (one male, one female, five gender unknown) between 6 June and 22 July. Juvenile owls were captured using noose carpet traps (Mealey 1997, Millsap and Bear 1997) placed on the burrow mound and in the entrance of burrows. The average (± SD) weight of captured juvenile owls ($n = 7$) was 122.9 ± 10.3 g. Juvenile Burrowing Owls were fitted with necklace-style radio transmitters (AVM Instrument Company Ltd., Colfax, CA, USA). Prior to capture, juvenile owls were observed flying between their respective main and satellite burrows, and undertaking short flights within the improved pasture.

The maximum range of the receiver and transmitters during field tests was 1.61 km and the expected battery life was 160 days. Five randomly selected transmitters were tested to examine the precision of directional bearings with a resulting mean and standard deviation of 1.64 ± 4.13 degrees (White and Garrott 1990). The average weight of the transmitters was 4.9 g which was 4% of the average body mass of the seven juvenile Burrowing Owls marked.

We attempted to locate radio-marked Burrowing Owls once each day between 1000 and 2000 hrs (EST) from 7 June to 10 October. Relocations were attempted between 2100 and 0500 hrs on 1–2 August to document activity and location of each owl during the evening and early morning. Radio tracking was conducted along all road and trails within Rutland Ranch when any radio-marked owl was not relocated during the day and evening telemetry sessions in the improved pasture. Once an

TABLE 1. Kernel home range estimates of juvenile Burrowing Owls within improved pasture, Bradenton, Florida, 2004.

Bird #	Relocations	95% Kernel home range (m^2)	75% Kernel home range (m^2)	50% Kernel home range (m^2)
1	8	177	123	79
2	13	186	110	70
3	22	105	64	45
4	22	98	60	38
Mean		141	89	58

TABLE 2. Dispersal distance of juvenile Burrowing Owls from improved pasture, Bradenton, Florida, 2004.

			Distance from main burrow	
Bird #	Dates	Relocations	Min (m)	Max (m)
1	6 Aug–5 Oct	3	407	10,083
2	6 Aug–24 Sep	15	466	679
3	17 Aug	1	366	366
4	6–17 Aug	7	236	337

owl was not located after several attempts, the road network surrounding Rutland Ranch was surveyed at intervals of 0.80 km. Aerial telemetry was used to locate missing owls if an owl was still not located.

Program Animal Movement V.2 Beta (Hooge and Eichenlaub 1997) was used to estimate home ranges for each juvenile owl during the breeding period using the fixed kernel method with least squares cross validation as the smoothing parameter. The home range for each juvenile owl was calculated using relocations taken during daylight hours. Three separate home range estimates for each owl were calculated based on probabilities (95, 75, and 50%) of the estimated distribution of use. The measure tool in ArcMap 8.3 was used to calculate dispersal distance by measuring the distance (m) from each owl's location outside of the improved pasture to its respective main burrow.

RESULTS

Three radio-collared juveniles were killed by unknown predators. The four remaining owls were relocated 41 of 56 days radio tracking was attempted within the improved pasture. Radio tracking was not attempted during 2 days due to lightning and for 13 days because two stream crossings were flooded. The mean home ranges of the four juvenile Burrowing Owls, based on probabilities of 95, 75, and 50% of the estimated distribution of use were 141, 89, and 58 m^2, respectively (Table 1).

Two Burrowing Owls during night tracking sessions were near their main burrows at 2100 hrs, but no Burrowing Owls were located in the pasture after 2200 hrs. One Burrowing Owl was located at 2300 hrs, 264 m from its main burrow within the extensive patch of saw palmetto surrounding the pasture. Telemetry signals outside of the improved pasture were faint and brief making it difficult to triangulate the position of any owl. No signals were located after midnight in the improved pasture or from the trails surrounding it.

Burrowing Owls began dispersing from the improved pasture on 6 August when all burrows, except for a main and satellite burrow in the highest elevated area of the pasture, were flooded due to seasonal rainstorms. No juvenile owls could be located within Rutland Ranch or from the road network surrounding the property by 30 September.

Aerial surveys were conducted on 5 October within a radius of approximately 15 km of the improved pasture to locate the missing owls. One juvenile owl was relocated 10.1 km southeast of Rutland Ranch in habitat composed of predominantly scrub oak (W. D. Gordon, pers. comm.). Dispersal distance for juvenile owls varied (Table 2).

DISCUSSION

The home range estimates of juvenile Burrowing Owls post hatch indicates that juvenile owls are extremely dependent on main and satellite burrows. Dispersal of juvenile Burrowing Owls from habitat used post hatching coincided with flooding of the pasture and burrows beginning on 6 August. Juvenile owls were not relocated in the improved pasture after dispersal even after the pasture had dried. All four juvenile Burrowing Owls used the extensive saw palmetto patch surrounding the pasture during the day before dispersing beyond the range of the receiver. One juvenile owl was relocated near several live oaks (*Quercus virginiana*) growing near the improved pasture.

The large areas of private agricultural and pasture land surrounding Rutland Ranch, coupled with limited access to these properties, made it difficult to locate Burrowing Owls from the surrounding road network. Aerial telemetry, initiated after the owls had dispersed from the pasture, assisted in locating only one of four juvenile Burrowing Owls, possibly because of battery failure of the three remaining transmitters.

Knowledge of breeding and post-hatching habitat requirements of Burrowing Owls in rural environments (especially grazing lands and natural areas) is particularly important because of continued habitat loss due to increased growth and development throughout Florida. We also note that Burrowing Owl populations in urban areas such as vacant lots, college campuses, and private residences are also not immune to the effect of development. Urban areas may provide only temporary Burrowing Owl habitat due to the inverse relationship between the size and persistence of owl populations, and the level of human development (Courser 1976, Wesemann 1986, Millsap and Bear 2000).

The Burrowing Owl has been listed as a Species of Special Concern since 1979 by the Florida Fish and Wildlife Conservation Commission (Millsap 1997). Without conservation and management, Burrowing Owls may become a state listed threatened species because of vulnerability to habitat modification, environmental alteration, human disturbance, or human exploitation (Florida Fish and Wildlife Conservation Commission 2004b). A greater understanding of Burrowing Owl ecology in rural environments is needed to successfully manage and conserve this species throughout Florida.

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American White Pelicans Force Copulations with Nestlings

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ABSTRACT.—We observed 56 forced copulation (FC) events in a breeding colony of American White Pelicans (*Pelecanus erythrorhynchos*) in Saskatchewan, Canada during the 2005 nesting season. All FCs were directed at nestlings >21 days of age that were not continuously attended by an adult. The onset of FCs occurred in close synchrony with an unexpected late-season increase in adult copulation attempts. We suggest that FC directed at nestlings is not simply an aberrant and nonadaptive behavior. Rather, copulations with nestlings result from adult male pelicans being inappropriately stimulated to copulate with nestlings when actually seeking copulations with adult females. *Received 22 December 2005. Accepted 24 July 2006.*

Forced copulation is a behavior used by males of some species as a strategy to fertilize females that would otherwise be unreceptive (McKinney et al. 1983). The proportion of fertilization events gained via forced copulations is likely low (e.g., 2–5%; Dunn et al. 1999), but this behavior is generally considered adaptive and has been reported for several avian orders (e.g., Anseriformes, McKinney et al. 1983; Charadriiformes, Ewins 1993; Passeriformes, Rising and Flood 1998; and Galliformes, Giudice and Ratti 2001). On rare occasions, forced copulation attempts by adults are directed toward conspecific young. We found a small number of reports of adults attempting to copulate with fledged conspecific juveniles (Armstrong 1988, Ewen and Armstrong 2002) and with unfledged chicks (Kinkel and Southern 1978, Besnard et al. 2002). Fledged juveniles may be mistaken for adult females in some species, but there is no obvious adaptive explanation for forced copulations with unfledged chicks. The motivation for forced copulation with unfledged chicks is therefore unclear.

We describe patterns associated with forced copulation attempts on chicks by adult American White Pelicans (*Pelecanus erythrorhynchos*; hereafter pelicans) in a breeding colony

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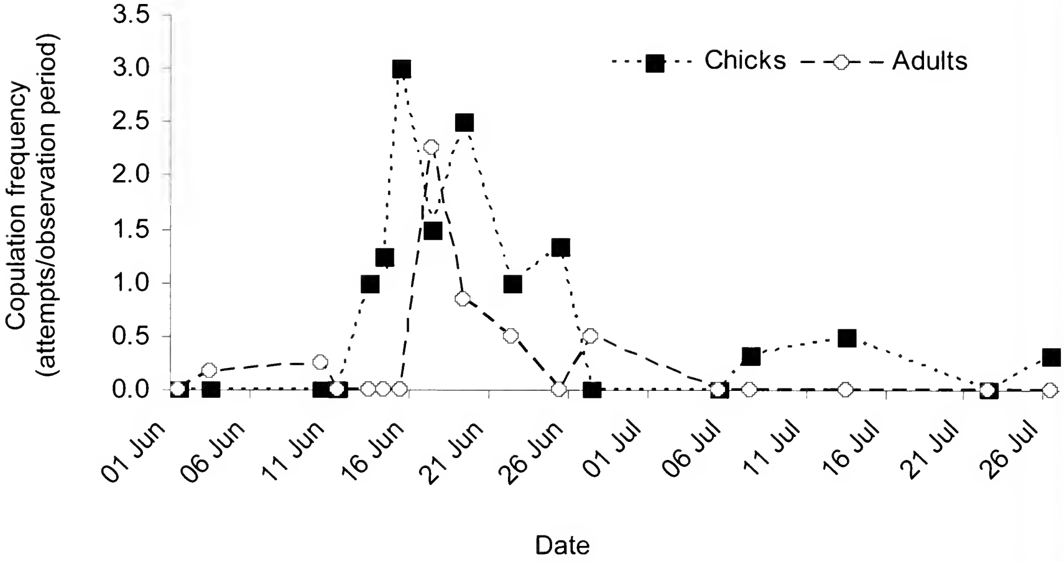

FIG. 1. Mean frequency of copulation attempts by adult American White Pelicans with other adults or with unfledged chicks at Last Mountain Lake National Wildlife Area and Migratory Bird Sanctuary, Saskatchewan in 2005. The data are expressed as the number of attempts per 30-min observation period. Means are based on two to six observation sessions per day; error bars have been omitted for clarity.

in Saskatchewan, Canada. To our knowledge, this behavior in pelicans has been reported anecdotally once previously (Schaller 1964) and remains poorly characterized for birds.

METHODS

We observed interactions between adult pelicans and chicks in breeding colonies on two islands in the Last Mountain Lake National Wildlife Area and Migratory Bird Sanctuary in Saskatchewan, Canada (51.1° N, 107.0° W). The islands were shared with breeding colonies of Double-crested Cormorants (*Phalacrocorax auritus*) and California Gulls (*Larus californicus*). We estimated there were 1,360 pelican nests on Island A (10.1 ha) and 240 nests on Island B (3.5 ha) from aerial photos taken on 6 June 2005. The islands were 680 and 550 m from shore, and were observed from the mainland using 45× and 30× spotting scopes, respectively. Two observers continuously monitored interactions in fields of view containing similar numbers of chicks for 30 min at a time. We performed two to six observation periods per day with the exception of 15 June 2005 when only a single 30-min session was possible due to inclement weather. We observed the islands for a total of 41.5 hrs between 1 June and 26 July 2005 and recorded all copulation attempts. We defined forced copulations (FC) with chicks as any interaction during which an adult attempted to mount, or actually mounted and copulated with, an unfledged nestling. In all FCs, nestlings appeared to resist the actions of adults by struggling not to be pinned and attempting to escape and/or dislodge the adult during copulation motions. Between 15 June and 5 July 2005, we visited the pelican colony on Island B on 5 days (two to four observers/visit; each visit lasted 12–20 min) to collect regurgitations from chicks as part of a diet study. We visited Island A once for 15 min (three observers) on 5 July 2005 to conduct a disease and mortality survey.

RESULTS

We observed a total of 56 FCs that began on 13 June, peaked on 15 June, and declined thereafter (Fig. 1). FCs were first observed when a large proportion of the chicks were approximately 3 weeks of age and formed pods in which they were not continuously attended by a parent, and continued until chicks were near fledging. We were unable to estimate the total number of adults and chicks involved in FCs over the season because individual birds were not uniquely marked.

However, we were able to distinguish between independent FCs during each 30-min observation session because of our continuous monitoring approach. The number of adults involved in FCs in each observation period ranged from one to three, and the number of targeted chicks ranged from one to five. There were 13 30-min sessions in which a single FC was detected involving one adult and one chick. In 11 sessions we detected multiple FC events (up to a maximum of six) involving two to three adults and two to five chicks. In these sessions, 23% (range 0–67%) of the total FCs in each session were repeated events initiated by the same adults. Similarly, 12% (range 0–33%) of FCs in each session were experienced by the same chick that was targeted several times.

We were able to view and record details of adult behavior in 34 FCs. In the remaining 22 events we were unable to clearly see the behavior of the adults preceding the FC. Of the 34 FC interactions characterized, 12 (35%) involved adults seeking out an isolated chick that was not part of a pod, and violently jabbing and biting it. The adult then forced the chick to the ground and pinned it by the neck or back of the head using its bill, followed by attempted mounting and/or copulation movements lasting approximately 15–30 sec. In 11 of 34 (32%) FCs, adults first actively isolated chicks by disrupting pods using violent bill jabbing. Once a chick was accessible, FCs occurred as described above. Before and/or after 9 of 34 (27%) FCs, adult pelicans appeared to be tending chicks. In these nine cases, adults preened the chicks before pinning them and attempting to copulate and, in some cases, adults continued to preen and/or sun-shade chicks afterwards. In 2 of 34 (6%) instances, we observed an FC followed by the adult feeding the chick. In all cases, chicks visibly resisted adults attempting FCs, struggling not to be pinned, and attempting to dislodge the adult during copulation motions. We were unable to ascertain whether cloacal contact occurred between adults and chicks during any of the observed FC events.

Adult pelicans began initiating copulations with other adults on 17 June 2005 (Fig. 1; $n = 20$ instances observed). This behavior was unexpected given the colony was well beyond the stage of nest establishment, with more than 90% of nests into the chick-rearing phase and only several small sub-colonies that were late in egg incubation. When the pattern of copulation events was considered separately by island, FCs were split evenly between islands (28/56, or 50% on each island). In contrast, 16 of 20 (80%) of the adult copulation attempts occurred on Island B, compared to only 4 of 20 (20%) on Island A (Fig. 2A, B). Adult copulations began concurrently with the appearance of a group of adult pelicans standing near some of the later nesting birds incubating eggs on Island B. This group of birds engaged in frequent courtship displays (e.g., head up with pouch flaring, and strut-walking; Knopf 2004). On at least one occasion, a male pelican from this group attempted to copulate with an unreceptive adult sitting on a nearby nest.

DISCUSSION

Based on a small number ($n = 23$) of FC observations, Schaller (1964) proposed that movements of nestling pelicans might resemble those of receptive females, thus stimulating sexual behavior in adult males. However, that study provided no quantitative data on FC timing or frequency, and the observations did not permit establishment of any link between FC events and adult copulation behavior. In our study, the similarity in the date of onset of both FCs and adult copulations suggests a relationship between these two behaviors. We postulate that FCs represent adult male pelicans directing inappropriate sexual attention towards nestlings when actually seeking to copulate with adult females. If this is the case, FCs in pelicans can be interpreted as a non-adaptive by-product of potentially adaptive adult copulation attempts, as opposed to simply aberrant behavior. Thus, we expect FC behavior to be widespread in pelican colonies.

It is not clear why some adult pelicans began courtship and copulation attempts, including FCs, at our study site in mid-June. This is well beyond the nest-establishment period on the observed islands where even the latest sub-colonies to begin nesting were at least 3 weeks into egg incubation. Besnard et al. (2002) suggested the high frequency of FC observed in Black-billed Gulls (*Larus bulleri*) was a direct result of a flooding event that destroyed part of the colony. Nest loss asso-

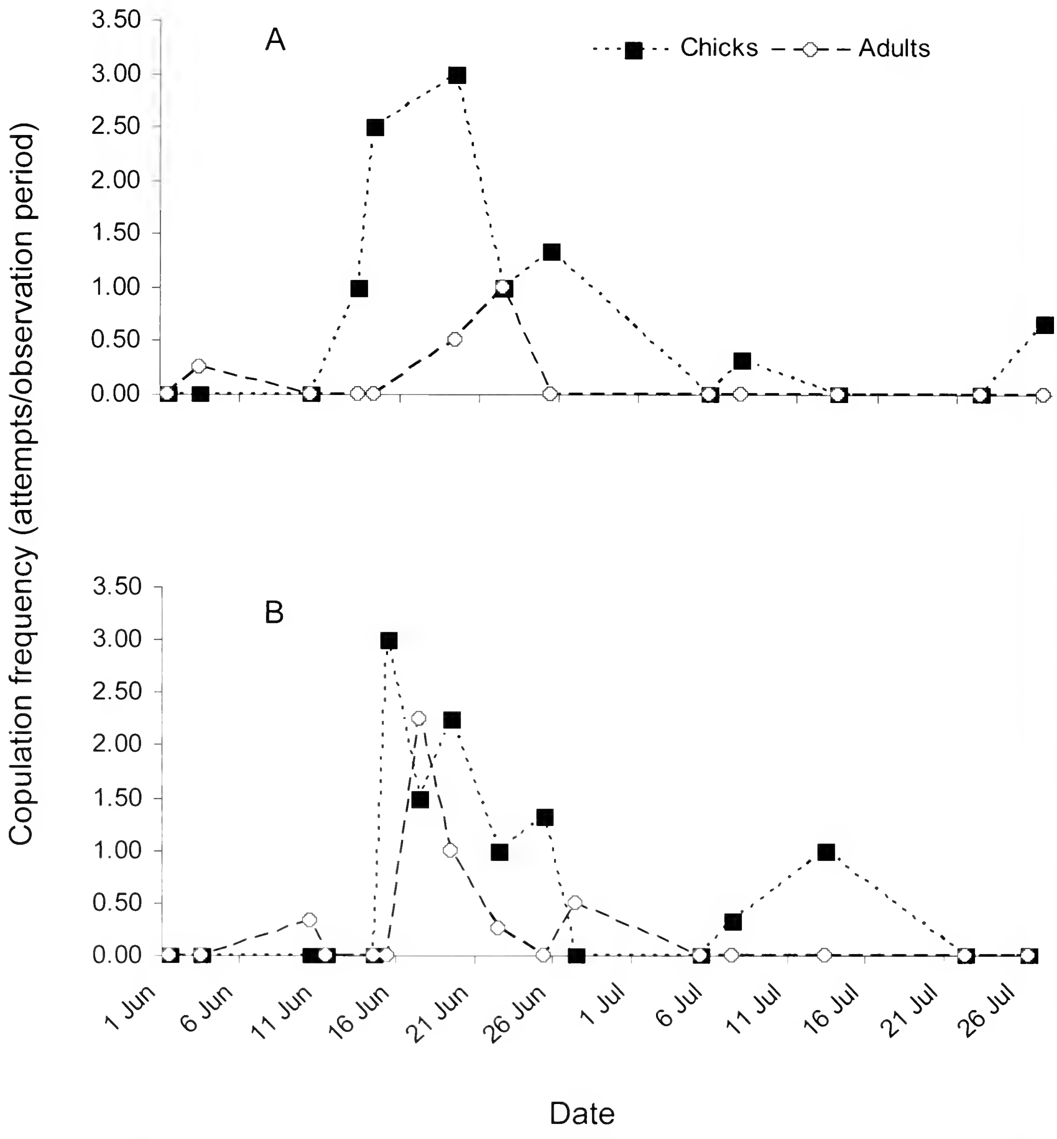

FIG. 2. Mean frequency of observed copulation attempts by adult American White Pelicans with other adults or with unfledged chicks in (A) a primarily undisturbed colony on Island A, and (B) a colony on Island B at Last Mountain Lake National Wildlife Area and Migratory Bird Sanctuary, disturbed five times between 15 June and 5 July 2005 for collection of diet samples. The data are expressed as the number of attempts per 30-min observation period. Means are based on two to six observation sessions per day; error bars have been omitted for clarity.

ciated with the flood stimulated large-scale and intensive re-nesting, placing nestlings in the colony concurrent with courting and copulating adults. Re-nesting male gulls directed inappropriate sexual attention towards chicks begging for food, which resembles female solicitation in that species. It is therefore possible that disturbance and nest loss may be a prelude to FCs.

In our study, the only disturbances of which we are aware were our five visits to Island B between 15 June and 5 July 2005, and the single visit to Island A on 5 July 2005. FC frequency peaked on 15 June, and most adult copulations were observed between 17 and 22 June on the more disturbed Island B. This raises the possibility that our research activities indirectly caused the associated FC behavior. On Island B, we documented the loss of 12 of 240 (5%) pelican nests due to depredation of young chicks by California Gulls during our first two visits. By the time we visited Island A, however, all chicks were too large to be at risk of gull depredation. It seems unlikely this small level of nest loss and potential re-nesting by the associated adult pelicans can explain the number of FC events we observed. In addition, individual pelicans typically abandon colonies following nest loss rather than attempting to re-nest within a season (Schaller 1964), and it is extremely unlikely that a re-nesting response could be induced so quickly following the first disturbance event. Preliminary observations of three FC events in early June 2005, in the absence of any colony disturbance, support the idea that disturbance is likely not the major cause of the behavior.

An alternative explanation for the sudden appearance of courtship behavior, adult copulations, and FCs in mid-June is the possibility that birds were still attempting to join the colony despite its advanced state, or that non-breeding adults entered the colony to 'practice' copulation. A further point worth considering is that while we have assumed FCs to be instigated by adult male pelicans, Kinkel and Southern (1978) reported forced copulation attempts on chicks by adult female Ring-billed Gulls (*Larus delawarensis*), suggesting this assumption could be erroneous. We conclude that FCs occur in pelicans and appear to be non-adaptive, and associated with adult copulation activity. The circumstances surrounding the stimulation of FC behavior and the extent to which it occurs in other colonies and other species requires further investigation.

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Humboldt Penguins (*Spheniscus humboldti*) in the Northern Hemisphere

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ABSTRACT.—Penguins, Southern Hemisphere birds, were introduced to the Northern Hemisphere several times in the 1930s. None of the four species introduced became established but some individuals survived for at least a decade. Humboldt Penguins (*Spheniscus humboldti*) were observed in waters off the west coast of North America several times in the 1970s and 1980s and one was caught in a fishing net in Alaska in 2002. Penguins theoretically might be able to swim to suitable habitat in the Northern Hemisphere, but we argue the most likely explanation for their arrival in the Pacific Northwest was by fishing boat. *Received 21 October 2005. Accepted 3 September 2006.*

On 18 July 2002, salmon fisherman Guy Demmert caught an adult Humboldt Penguin (*Spheniscus humboldti*) in his purse seine net off Noyes Island, Alaska (55° 30′ N, 133° 40′ W), nearly 10,000 km from its native range in Peru and Chile (from 5° S to 42° S). The penguin appeared healthy and robust, and was released unhurt after being photographed (Guy Demmert, pers. comm.) (Fig. 1). This may not have been the first sighting of penguins in Alaska. A 1976 research cruise in the Gulf of Alaska recorded "brown penguins" (M. J. Rauzon, pers. comm.), and Guy Demmert (pers. comm.) saw a penguin while fishing in 2001.

There are four earlier observations of Humboldt Penguins along the west coast of North America. In 1944, a single penguin was seen in the Queen Charlotte Islands (Beurling 1978); another was observed in 1975 near Long Beach, Washington (Campbell et al. 1990). There were three reports in 1978 of one to three Humboldt Penguins on northern Vancouver Island (Burnes 1978) with pictures of the penguins published in regional newspapers (Anonymous 1978b). One was seen in 1985 off the Washington coast (Campbell et al. 1990).

The only penguin species known to breed in the Northern Hemisphere is the Galapagos Penguin (*S. mendiculus*), with a few dozen pairs just north of the equator on Isabella Island (Boersma 1977). All other penguin species are confined to the Southern Hemisphere. The absence of penguins in the Northern Hemisphere is generally attributed to a combination of history and climate; the ancestors of penguins evolved in the Southern Hemisphere, and thermal and productivity barriers prevented them from moving northward (Sparks and Soper 1987, Soper 2000). Penguins require cool productive water to survive (Williams 1995) and are limited to areas where water temperatures do not exceed 20° C (Sparks and Soper 1987, Soper 2000). Even the Galapagos Penguin is mainly restricted to productive cold water (Boersma 1978).

We compiled reports of penguins in the Northern Hemisphere, and addressed three possible mechanisms explaining the presence of Humboldt Penguins in the north Pacific: (1) naturally occurring vagrant, (2) escape from Northern Hemisphere zoos, and (3) intentional release into the wild.

Naturally Occurring Vagrant.—Reports of vagrant penguins (e.g., outside their normal range) are not uncommon within the Southern Hemisphere. Macaroni (*Eudyptes chrysolophus*), Rockhopper (*E. chrysocome*), and King (*Aptenodytes patagonicus*) penguins have rested on beaches at Punta Tombo, Argentina, hundreds of nautical miles from breeding colonies (PDB, pers. obs.). Juvenile King Penguins were seen molting near Palmer Station, Antarctica in January 2001 and 2002, more than 1,300 km from the nearest breeding colony (PDB, pers. obs.). In extreme examples, Yellow-eyed (*Megadyptes antipodes*) and Erect-crested (*E. sclateri*) penguins were seen in the Falkland Islands, more than 8,000 km (4,300 nautical miles) from their breeding areas in New Zealand (Harrison 1983, Strange 1992), and Little Penguins (*Eudyptula minor*) were observed in Chile, 10,000 km (5,400 nautical miles) from their native range (Valverde and Oyarzo 1999, Brito 2000, Wilson et al. 2000).

The distances traveled by these individuals

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FIG. 1. Humboldt Penguin caught by salmon fisherman Guy Demmert on 18 July 2002 near Noyes Island, Alaska (photograph by Darin Fordyce).

is comparable to a Humboldt Penguin swimming from Peru or Chile to Alaska (~10,000 km), but the marine environments each would need to traverse are different. A penguin could complete the journey from New Zealand to the Falkland Islands by exploiting the Antarctic Circumpolar Current with its ample prey resources and without experiencing water temperatures in excess of 10–15° C (Duxbury and Duxbury 1994, Christoph et al. 1998). In contrast, a Humboldt Penguin swimming to Alaska would need to cross 4,500 km of mostly unproductive water between 20 and 35° C without the aid of currents (Lalli and Parsons 1997).

Primary production in the eastern tropical equatorial and north Pacific averages 80 g C/m^2/year (grams of carbon/meter^2 per year), much lower than the 350 g C/m^2/year in the upwelling regions where Humboldt Penguins live and breed (Duxbury and Duxbury 1994). However, coastal productivity averages 150 g C/m^2/year with areas along the west coast of the United States as high as 350 g C/m^2/year (Duxbury and Duxbury 1994). Eddies, shelf breaks, river plumes, and tidal fronts may also provide local concentrations of phytoplankton that can be exploited by zooplankton and their larger predators (Lalli and Parsons 1997). Thus, a Humboldt Penguin could potentially find sufficient food by remaining close to the eastern Pacific coast. However, a bird following this route should be conspicuous while resting on the beach—especially along the crowded coast of California—and no Humboldt Penguins have been reported to the California bird records committee (Philip Unitt, pers. comm.).

A Humboldt Penguin crossing through equatorial waters would also face a thermal barrier. Penguins thermoregulate in the cold waters of their native ranges by a combination of subcutaneous fat deposits and dense overlapping feathers that prevent water from reaching the skin surface. In warm weather, while on land, these same attributes can cause penguins to overheat and die (Boersma 1974a, Simeone et al. 2004). The upper limit of a Humboldt Penguin's thermoneutral zone is approximately 30° C (Drent and Stonehouse 1971) and, on land, Humboldt Penguins at rest use evaporative heat loss via body positioning or panting to avoid heat stress in temperatures exceeding 25–30° C (Simeone et al. 2004). In crossing the equator, Humboldt Penguins would experience water and air temperatures in excess of 30° C, and active swimming would further increase the heat load by generating metabolic heat. A penguin in warm water would be restricted to panting to eliminate excess heat, which would prevent the bird from either foraging or transiting. Thus, while a Humboldt Penguin traveling from Peru or Chile to Alaska might be able to find food, it would probably not survive the high tropical temperatures.

Escape from Northern Hemisphere Zoos.—Penguins do escape from zoos: on 9 August 2002 a Magellanic Penguin (*S. magellanicus*) chick was reported missing from the Point Defiance Zoo in Tacoma (Anonymous 2002). It was thought to have escaped to Puget Sound and "fledged." Whether it did or not is unknown, as it was not seen again and no corpse was found. An African Penguin (*S. demersus*) seen 3–16 February 1981 near Chimney Rock, Pt. Reyes, California, likely escaped from a California zoo (Pyle and McCaskie 1992). Notably, no penguins were reported as escaped prior to the repeated Humboldt Penguin sightings near Vancouver Island in 1978 (Burnes 1978).

Humboldt Penguins are kept in more zoos (approximately 150 worldwide) than any other penguin species (International Species Information System 2005). Over 2,000 Humboldt Penguins are kept in zoos and aquariums in Japan alone, more than in any other country (Boersma 1991). Zoos typically use permanent bands or tags to mark their penguins. None of the Humboldt Penguins observed in the north Pacific (including the one captured by fisherman Demmert) was marked, suggesting they were not zoo escapees. The possibility that Humboldt Penguins escaped unmarked and unreported cannot be excluded, but there is no independent evidence supporting introduction to the wild from captive zoo populations.

Intentional Release into the Wild.—Introductions of penguins into the Northern Hemisphere have occurred, but none established self-sustaining populations. In August 1936, Carl Schøyen of Norway's Nature Protection Society released nine King Penguins at Gjæsvær, West Finmark, and Røst, Lofoten (Lund 1953, Curry-Lindahl 1963, Sparks and Soper 1987). Four of the birds were captured and killed within 1 year. On 31 May 1944, a single individual was seen alive at Breistrand, Vesterålen, almost 8 years after its release (Curry-Lindahl 1963). Gentoo (*Pygoscelis papau*) and Macaroni penguins were also introduced at Røst, Lofoten in 1938, but all were dead by the following year (Blædel 1963). Norway's Nature Protection Society may have released several African Penguins, also in 1938 (Sparks and Soper 1987). The last penguin (species unknown) reported in Norway was seen on 2 July 1954, at Selsøyodden in Hamarøy (Sparks and Soper 1987).

There is indirect evidence that penguins may also be transported and released capriciously by fishermen and boaters. Live penguins are sometimes kept on shipboard by fishers (PDB, pers. obs.). In 1978, a Japanese trawler visiting Halifax, Nova Scotia had on board two King Penguins caught in nets when they were fishing in the Southern Ocean (Anonymous 1978a). Local fishermen in Peru capture and use Humboldt Penguins as bait (Patricia Majluf, pers. comm.). On 2 September 1961, a Rockhopper Penguin captured in a salmon net near Pukaviken, Blekinge, Sweden (Nilsson and Lundgren 1993) likely traveled from the Southern Ocean on a USSR fishing/whaling vessel returning to the fleet port at Kaliningrad (Magnus Forsberg, pers. comm.). The Humboldt Penguins seen off Washington and British Columbia were thought to have been brought from South America as fishermen's pets (M. C. E. McNall, pers. comm.). A Galapagos Penguin found dead on the coast of Panama (Eisenmann 1956) was probably picked up in the Galapagos by a pleasure boater who released it upon arrival in Panama—this is a common route that boaters often follow (Boersma 1974b).

Could the Humboldt Penguin captured in Alaska have come by boat? In the mid- to late 1970s, tuna vessels fished along the west coast of the Americas from northern Chile to California (Inter-American Tropical Tuna Commission 1979, 1980). The Humboldt Penguins seen off Vancouver Island in 1978 could have traveled by tuna boat from Peru or Chile, being released before the boats docked in Seattle. Seiners converting to Alaska crab boats in the late 1970s after the crash of the Peruvian anchovy fishery might also have brought Humboldt Penguins northward (M. A. Hall, pers. comm.). Boaters transporting penguins might have jettisoned the birds as they approached United States or Canadian ports for fear of prosecution under wildlife or health laws.

DISCUSSION

It seems unlikely that a Humboldt Penguin would swim nearly 90 degrees latitude (over 5,400 nautical miles) from Peru or Chile to Alaska. The lack of identification tags or reports of escapees suggests the penguins seen in Washington, British Columbia, and Alaska were not zoo birds. The most parsimonious explanation for a Humboldt Penguin reaching the Northern Hemisphere is that it got a lift on a boat. If the penguin captured by Demmert was brought by boat to Alaska, the question is when. *Spheniscus* penguins can live more than 25 years in the wild and as much as 36 years in zoos. It is possible the Humboldt Penguins that mysteriously appeared near Vancouver Island in 1978 were seen in Washington waters in 1985, and finally reached Alaska in 2002.

In the Northern Hemisphere, alcids are the ecological equivalent of penguins and, like penguins, are largely confined to areas of high productivity. The north Pacific has conditions suitable for penguin survival (Sparks and Soper 1987). As a temperate species, Humboldt Penguins would be physiologically well-adapted to conditions in the temperate north Pacific with its cold and productive waters similar to those in the upwelling region of the Humboldt Current off Peru and Chile. The Humboldt Penguin captured in Alaska may have been feeding on herring (*Clupea harengus pallasii*), a fish ecologically analogous to the anchovies it would find in its native waters. Temperate penguins (Humboldt, African, Magellanic) persist well in open-air Northern Hemisphere zoos where they are protected from predators and provided food. Their breeding and molt seasons become shifted within approximately 1 year and they follow their typical seasonal schedule (e.g., breeding in the northern spring). Scotland's Edinburgh Zoo has been successfully breeding sub-Antarctic penguins in outdoor pens since 1919 (Sparks and Soper 1987).

Penguins can survive in the wild in the Northern Hemisphere, but whether they can establish themselves remains an academic question. Of the penguins released in Norway, one pair (probably Kings) was reported brooding an egg at Sandholmen in 1944. One penguin was later killed by a fisherman and thought on inspection (and consumption) to be a young bird (Lund 1953). In 1948, a penguin fledgling (species unknown) was supposedly found, adopted, and cared for by a Sund, Lofoten man (Lund 1953).

Introductions are likely to continue as people move species around the globe, but it seems improbable that penguins will become established in the Northern Hemisphere for two reasons. First, so few are introduced and penguins breed more successfully in large groups (Boersma 1991). Second, the Northern Hemisphere has mammalian predators like bears (*Ursus* spp.), which the Southern Hemisphere lacks in coastal regions (the Spectacled Bear, *Tremarctos ornatus*, is mostly restricted to the Andes; Servheen et al. 1999). Predation is a concern for introduced penguins, as one of the Humboldt Penguins seen in British Columbia was captured and eaten by an eagle (Beurling 1978). Problems associated with small population size and predators will likely prevent any penguin species from colonizing the Northern Hemisphere, despite the fact they can survive for many years in the productive waters of the temperate north.

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Bilateral Gynandromorphy in a White-ruffed Manakin (*Corapipo altera*)

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ABSTRACT.—We report bilateral gynandromorphy in a White-ruffed Manakin (*Corapipo altera*) collected near Santa Fé, Panamá in 2004. The specimen had an oviduct and ovary on the left side and a single testis on the right. The plumage was phenotypically female on the right side and male on the left. The weight and genetic affinity of the specimen were characteristically female. Both Z and W chromosomes were detected in genetic samples from multiple tissue types and toe pads from both feet. This report is a novel record of gynandromorphy in a suboscine passerine. *Received 22 July 2006. Accepted 10 September 2006.*

Gynandromorphy is a rare state in which an individual exhibits both male and female traits. This condition often results in a clear bilateral demarcation of male and female morphology in sexually dimorphic species with bilateral symmetry. Gynandromorphy is rare in birds, but has been observed in a number of avian families, and is most commonly re-

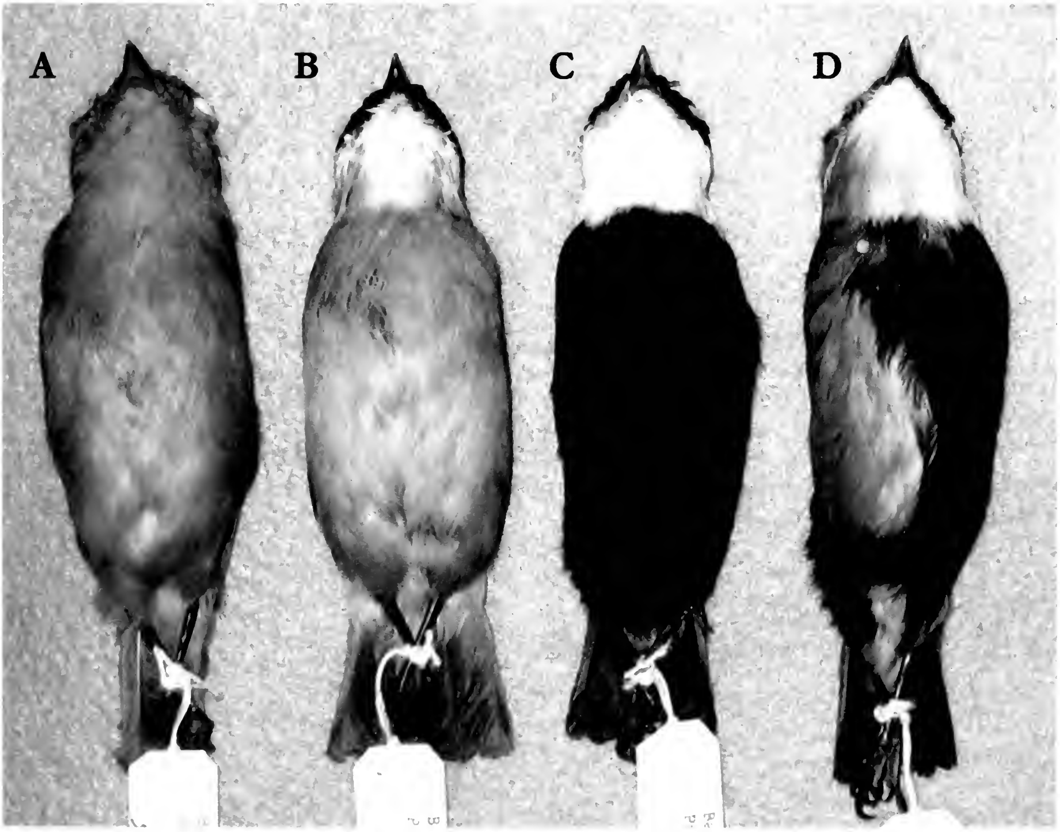

FIG. 1. Ventral views of female (A), immature male (B), mature male (C), and bilateral gynandromorph (D) White-ruffed Manakin skins.

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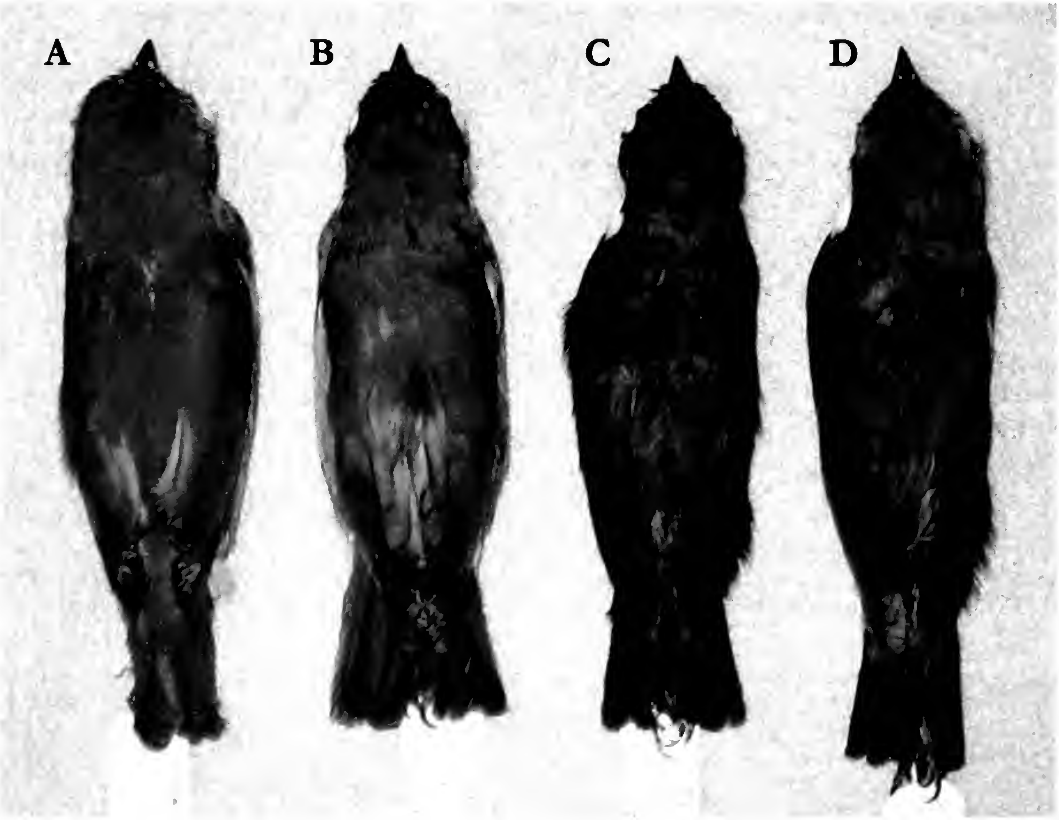

FIG. 2. Dorsal views of female (A), immature male (B), mature male (C), and bilateral gynandromorph (D) White-ruffed Manakin skins.

ported in the Fringillidae (Kumerloeve 1987, Patten 1993). The general pattern in gynandromorphs is female plumage characters on the left side and male characters on the right, corresponding to the orientation of the ovary and testis in birds (Crew and Munroe 1938, Kumerloeve 1954). The plumage patterns of avian gynandromorphs can be driven by genetic or hormonal factors, although direct mechanisms are not well known; it is possible that a variety of pathways can lead to the condition (Graves et al. 1996).

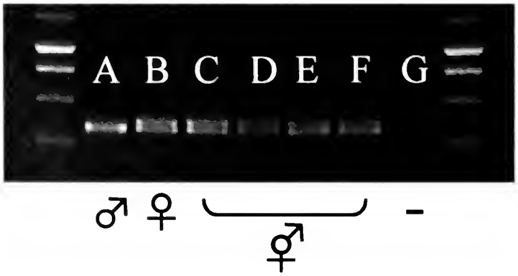

FIG. 3. Gel electrophoresis of amplified CHD products. Male heart (A), female heart (B), and negative (G) controls were run with gynandromorph products from heart (C), pectoral muscle (D), left (E), and right (F) toe pads.

A White-ruffed Manakin (*Corapipo altera*) bilateral gynandromorph was collected on 3 March 2004 near Santa Fé, Panamá during a scientific expedition co-sponsored by the Barrick Museum of Natural History (MBM) and the Smithsonian Tropical Research Institute. The bird was collected during passive mist netting and was not observed before its capture. This specimen was deposited in the MBM (voucher MBM 15715) and represents the first record of a bilateral gynandromorph in a suboscine passerine.

Mature male White-ruffed Manakins have a glossy blue-black plumage with white undertail coverts and throat. Females are mostly olive green with a pale gray throat, while immature males have a patchy appearance where blue-black feathers are mixed with a generally olive green plumage (Snow 2004). The ventral side of the gynandromorph specimen has male plumage characters on the left side and female characters on the right (Fig. 1). This configuration is "reversed" in regards to the orientation of the gonads, which is a rare condition for avian gynandromorphs (Kumerloeve 1954). There is some overflow of sexual traits across the bilateral line with mostly male traits extending toward the right side. The dorsal side of the specimen has a mosaic of male and female colors throughout (Fig. 2), similar to known specimens of Evening Grosbeak (*Coccothraustes vespertinus*) gynandromorphs (Laybourne 1967).

Female White-ruffed Manakins are generally larger than males, but there is considerable overlap in wing, tail, and tarsus measurements (Wetmore 1972). Weights (mean ± SD) for a series of males (10.99 ± 0.69 g, $n = 16$) and females (12.69 ± 0.96 g, $n = 12$) were measured in the field during the same expedition; females had significantly greater mass (two-tailed independent t-test, $t_{25} = -5.36$, $P < 0.001$). The gynandromorph specimen weighed 13.1 g, differing from the distribution of male weights ($P = 0.001$) but not from females ($P = 0.33$). An oviduct and granular ovary (7.0×3.5 mm) were observed on the left side with a testis (2.5×1.5 mm) on the right side. During preparation of the gynandromorph specimen, three MBM staff verified observations of both male and female gonads. The specimen had a fully ossified skull and internal organs appeared normal with pectoral muscle, liver, and heart samples collected and frozen.

The genetic affinity of the specimen was assessed by amplification of the sex-linked chromo-helicase-DNA-binding (CHD) genes (Griffiths et al. 1998). The utility of the CHD protocol was tested in this species with male and female controls, which produced single and double bands, respectively. DNA was extracted from heart, pectoral muscle, and toe pad samples of the left and right foot of the gynandromorph. All samples produced double bands, indicating a female genetic affinity (ZW) throughout the body (Fig. 3).

This is the first record of bilateral gynandromorphy in Pipridae, but this condition could be easily overlooked in the field. Immature male White-ruffed Manakins look like females or display a mosaic of female and male plumage characters making the detection of a gynandromorph difficult in the field. Manakins are well known for their lekking behavior and courtship displays, and White-ruffed Manakin males engage in a variety of solitary and coordinated displays (Rosselli et al. 2002). It is unknown how this, or other, gynandromorphic Pipridae might behave in such a system.

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First Record of the White-tipped Sicklebill (*Eutoxeres aquila aquila*: Trochilidae) for Venezuela

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ABSTRACT.—A female White-tipped Sicklebill (*Eutoxeres aquila aquila*) was caught on 3 February 2006 at 1,050 m elevation in Agua Blanca, Municipio Andrés Bello, Mérida, Venezuela, 2 km southeast of La Azulita. This account represents the first record of this hummingbird species in Venezuela, extending the taxon's known distribution at least 500 km northeastward. *Received 23 February 2006. Accepted 11 September 2006.*

The White-tipped Sicklebill (*Eutoxeres aquila*) is a resident species in Central America from Costa Rica to Panama, in South America from the Colombian Pacific slope to northwestern Ecuador, and from the eastern slope of the Colombian Andes to northern Peru (Hilty and Brown 1986, Schuchmann 1999, Zamora et al. 2004). The altitudinal range is from sea-level to 2,100 m (Hilty and Brown 1986, Mazariegos 2000, Ridgely and Greenfield 2001, Zamora et al. 2004). Throughout most of its range, *E. aquila* inhabits the understory of humid forest, including second-growth forest and forest edges (Hilty and Brown 1986, Ridgely and Gwynne 1989, Stiles and Skutch 1989). It feeds mainly on *Heliconia*, *Columnea*, and *Centropogon* spp. (Borgella and Snow 2001, Zamora et al. 2004), and is frequently seen near patches of *Heliconia* spp. (Stiles 1975, Hilty and Brown 1986, Gill 1987, Ridgely and Gwynne 1989, Stiles and Skutch 1989, Borgella and Snow 2001).

A female White-tipped Sicklebill (Fig. 1) was mist-netted and collected on 3 February 2006 at Agua Blanca, 1,050 m elevation, 8° 42′ 32″ N, 71° 25′ 55″ W, Municipio Andrés Bello, Mérida, Venezuela, 2 km southeast of the town of La Azulita (Fig. 2). The vegetation at the capture site is predominantly second-growth forest surrounded by shade coffee plantations where *Miconia*, *Erythrina*, *Heliconia*, *Inga*, and *Heliocarpus* spp. are abundant. The forest stand is adjacent to La Sierra de la Culata National Park, an area comprising 200,400 ha of contiguous primary forest. The landscape surrounding the forest stand is characterized by a variety of land uses, including pasture, coffee plantations, farms, and towns. Annual mean temperatures oscillate between 10 and 18° C, with day-night amplitudes of 6–8° C, and annual rainfall varying from 100 to 260 cm (Ataroff and Sarmiento 2003). The vicinity of La Azulita is a hotspot for migratory and resident bird taxa in this Andean region; 456 species have been recorded in this area (Rengifo et al. 2005).

Our capture represents the first record of *E. aquila* for Venezuela (Phelps and De Schauensee 1979, Hilty 2003, Rengifo et al. 2005), extending the known distribution of this taxon at least 500 km northeastward from the closest location on the eastern slope of the Colombia Andes in the Cundinamarca Department (Hilty and Brown 1986). The individual captured had a strongly decurved bill (typical for the genus) and was bronzy green above, dark green on the crown and nape, heavily streaked (sooty and white) below, with a bifurcated tail which was bronzy green and broadly tipped with white. Measurements from the living individual were: total length 125 mm, wing chord 69.5 mm, tail 74.6 mm, bill 30.2 mm, tarsus 9.6 mm, and body mass 9.2 g. The specimen was prepared as a round skin and deposited in the Colección de Vertebrados de la Universidad de los Andes, Facultad de

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FIG. 1. Female White-tipped Sicklebill captured 3 February 2006 at Agua Blanca, Municipio Andrés Bello, Mérida, Venezuela.

Ciencias in Mérida, Venezuela (CVULA-522).

The known subspecies of the White-tipped Sicklebill, *E. a. aquila* (Bourcier 1847), *E. a. heterura* (Gould 1868), and *E. a. salvini* (Gould 1868), show only slight morphological differences. Our specimen appears to represent the nominotypical form based on the prominent white tips to the rectrices and the bright orange-ochraceous edges of the undertail coverts (Schuchmann 1999). Of the three subspecies of *Eutoxeres aquila*, *E. a. aquila* would be most likely to occur in Venezuela, given its current distribution along the eastern Andes from Colombia to Peru (Schuchmann 1999, Mazariegos 2000). This mountain range is linked with the Venezuelan Andes by a faunal exchange corridor of submontane and seasonal forests, which form a relatively continuous belt across the Táchira low (Anderson and Soriano 1999, Soriano et al. 2005). Further studies will be needed to evaluate if the specimen of *E. aquila* is a member of an isolated relict population, part of a larger population continuous with Colombian populations, or even a new taxon.

Previous accounts of the natural history and ecology of *E. aquila* describe the species as a trapliner (foraging strategy used by pollinators in which they proceed from one plant to another, often over great distances; McDade 1992) with some altitudinal movement that depends on the flowering periods of *Heliconia* spp. (Musaceae; Ridgely and Gwynne 1989, Stiles and Skutch 1989, Mazariegos 2000, Borgella and Snow 2001, Zamora et al. 2004). We removed pollen grains from the hummingbird specimen following Kearns and Inouye (1993). They were subsequently identified to species level by comparison with samples of *Heliconia* spp. pollen collected in the same area. All of the pollen grains (n = 57) collected from the bird were from *Heliconia bihai*. This plant reaches heights of 2–3 m and may dominate the understory, especially along ridges where sufficient light is available (Aristeguieta 1961, Berry and Kress 1991). A large stand of this species occurred at the cap-

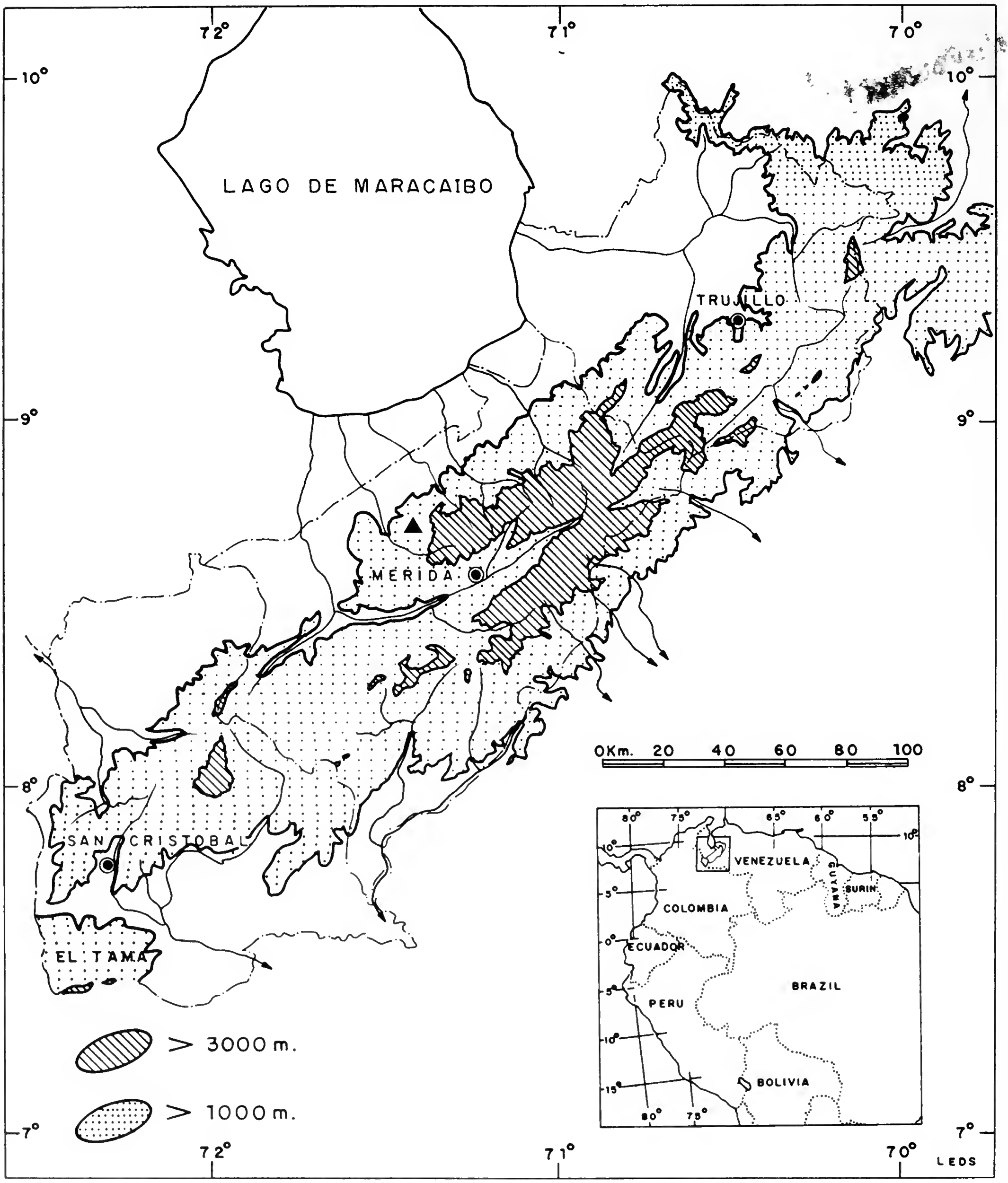

FIG. 2. General vicinity of Mérida, Venezuela. Solid black triangle indicates where the White-tipped Sicklebill was captured.

ture site, indicating it was an appropriate microhabitat for specialized avian visitors such as *Eutoxeres*.

ACKNOWLEDGMENTS

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Frequency of Injuries in Three Raptor Species Wintering in Northeastern Arkansas

Bryan E. Bedrosian[1,2,4] and Amy M. St.Pierre[1,3]

ABSTRACT.—It may be reasonable to assume that raptors would likely perish as the result of an injury that potentially impaired their ability to capture prey. We present results from 98 wild-caught raptors that support the converse claim: raptors can and do survive with many types of injuries. We report a conservative injury estimate of 14% for wintering populations of Red-tailed Hawks (*Buteo jamaicensis*), American Kestrels (*Falco sparverius*), and Cooper's Hawks (*Accipiter cooperii*) in northeastern Arkansas. Injuries in these species included broken or missing talons, ulcerative pododermatitis (bumblefoot), missing toes, healed wing fractures, and iris damage. *Received 11 October 2005. Accepted 29 July 2006.*

Raptors almost solely rely on live captures of potentially harmful prey (Gibson et al. 1998) and it seems reasonable to assume that a serious injury to an appendage or organ (e.g., eye) necessary for the successful capture of prey would ultimately result in the death of that individual (Cooper et al. 1980). There is often a need to rehabilitate injured birds because of injuries, both naturally and human inflicted (Ress and Guyer 2004). However, there is some evidence that birds with injuries can survive in the wild without rehabilitation (Blodget et al. 1990, Houston 1993, Murza et al. 2000, Roth et al. 2002, Tingay et al. 2004).

The frequency of injuries in raptors has been documented for Griffon Vultures (*Gyps fulvus*) (Houston 1993), North American accipiters (Roth et al. 2002), and American Kestrels (*Falco sparverius*) (Murza et al. 2000). The studies of vultures and accipiters quantified only healed fractures in the long bones and pectoral girdle, respectively. Murza et al. (2000) found an injury rate of 5.9% for wild-caught individuals in a Canadian population of American Kestrels. We present the occurrence of injuries in 98 wild-caught, wintering raptors in the delta region of Arkansas.

METHODS

Our study area included Craighead and Poinsett counties (35° 30′ 36″ N, 90° 36′ 91″ W) in northeastern Arkansas. The region is dominated by intensive agriculture, with interspersed small woodlots (typically <2 km^2). Major prey items for Red-tailed Hawks (*Buteo jamaicensis*) in the area included hispid cotton rats (*Sigmodon hispidus*) and marsh rice rats (*Oryzomys palustris*; BEB and AMS, pers. obs.). American Kestrels in the study area fed mainly on mice (*Peromyscus* spp.) and vole species (J. M. Learned, Arkansas State University, pers. comm.). The major prey species of Cooper's Hawks (*Accipiter cooperii*) are unknown, but assumed to be mainly Red-winged Blackbirds (*Aeglaius phoeniceus*) and other wintering songbirds.

We trapped, banded, and performed visual examinations of raptors during fall and winter 2002–03 and 2003–04. Raptors targeted for trapping and banding included Red-tailed Hawks, American Kestrels, and Cooper's Hawks for a concurrent winter ecology study. We trapped birds using (1) *bal-chatri* traps (Berger and Mueller 1959) using mammalian and avian baits, (2) bow-net traps and noose-harnesses baited with live Rock Pigeons (*Columba livia*) and European Starlings (*Sturnus vulgaris*), and (3) *dho-gaza* nets with a Great Horned Owl (*Bubo virginianus*) decoy (Jacobs 1996, Jacobs and Proudfoot 2002).

We estimated a keel/pectoral muscle mass index for a relative body condition index for each bird captured. The index was scored as (1) in superior condition if the keel felt indistinct between the pectoral muscles, (2) in average condition if the keel was noticeable, and (3) below average condition if the keel was distinct. We assigned ages to each bird as hatch-year or after-hatch-year based on plumage.

We used two-sample *t*-tests to test for dif-

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ferences in keel indices of injured and non-injured Red-tailed Hawks. We also created a body condition index using the residuals of a linear regression of tarsus length and mass (Webb et al. 2004). The regression of a structural body component and mass gave us an index of how much a hawk of a given size should weigh. If a bird had a negative residual from the tarsus length versus mass regression, it was considered to be in below-average condition. Conversely, if the residual was above the regression line (positive), the bird was considered in above-average condition. We used *t*-tests to compare residual condition indices of injured and non-injured Red-tailed Hawks.

We designated birds as injured if they had broken or missing talons, missing toes, healed fractures, or eye injuries. All of these conditions were considered injuries because of the potential vulnerability of hawks to attacks by prey, or if the condition could result in decreased hunting success. We did not perform complete physical examinations of all birds captured, nor did we use radiographs to examine for healed bone fractures. All injuries reported were opportunistically detected during routine banding and measuring processes; less obvious injuries were most likely overlooked. Thus, the injury estimates reported here are minimum values.

RESULTS

We trapped 98 raptors over the 2-year study period. We do not know if birds trapped were migrants or residents. Most birds captured were Red-tailed Hawks (n = 86, 43 juveniles and 43 after-hatch-year birds). We also captured seven American Kestrels and five Cooper's Hawks.

Fourteen percent of the raptors had injuries (Red-tailed Hawks—9%, kestrels—14%, and Cooper's Hawks—20%). We primarily focused on Red-tailed Hawk injuries because of the limited sample sizes for kestrels and Cooper's Hawks. We documented that 12% and 7% of captured juvenile and adult Red-tailed Hawks, respectively had injuries.

The keel indices of non-injured and injured Red-tailed Hawks did not differ (P = 0.18). We found no differences (P = 1.0) between body condition indices of the two groups (injured vs. non-injured) using the residuals of a mass versus tarsus length regression. Of the eight Red-tailed Hawks with injuries, six injuries were on the foot or leg and two occurred on the wing (one injured bird was re-captured with a different injury than during its first capture) (Table 1). There were two cases of ulcerative pododermatitis (i.e., bumblefoot), and both birds were classified as having Type II, characterized by the pronounced swelling on the affected foot. We captured one American Kestrel missing a leg and a digit on the remaining foot, and one Cooper's Hawk with a damaged iris sphincter (Table 1). All birds appeared to have incurred injury prior to trapping.

TABLE 1. Injuries observed (n) in wild-caught raptors in Arkansas during winters 2002–03 and 2003–04.

	Red-tailed Hawk	American Kestrel	Cooper's Hawk
Bumblefoot	2	[a]	[a]
Missing toe/leg	2[b]	1[c]	[a]
Broken talon	2	[a]	[a]
Healed wing fracture	2	[a]	[a]
Eye injury	[a]	[a]	1
Total captured	86	7	5

[a] Not observed.

[b] One bird was initially captured with a broken right #2 talon and was later recaptured (within the same year) with the right #2 toe missing. This bird is reported in both categories.

[c] This individual was missing its entire left leg and the #2 toe on its right leg.

DISCUSSION

We are not certain of the causes of injury for any of the birds captured. It is possible the injuries were caused by leg-hold traps set on poles for raptors (Durham 1981) or by other negative human interactions. It is also possible that some or all of the birds may have incurred injury during prey captures; some injuries may have been inadvertently self-afflicted. Our data suggest that injuries occur relatively frequently in wild raptors, irrespective of age. Injury rates have not been reported in previously studied populations of Red-tailed Hawks because most studies focus on breeding populations.

Our estimate of injured Red-tailed Hawks (9%) may be biased for two reasons. First, injured birds may be more prone to responding to a trap set, because of decreased hunting capabilities. We believe that our estimates are not biased due to decreased hunting abilities because if the injury caused a decrease in foraging success, the birds would exhibit below average body condition indices. The birds may have initially had decreased success following injury but all of the injuries observed were older and the birds were not in below-average condition. Second, we may have underestimated the frequency of injuries because we did not perform complete physical examinations on each individual after capture to feel for past breaks, skin lesions, or other inconspicuous injuries.

Documented injury percentages range from 6 to 20% for raptor and vulture species (Houston 1993, Murza et al. 2000, Roth et al. 2002, this study). Houston (1993) found the highest incidence of injuries in vultures (20%) by examining for healed fractures, and attributed the high frequency to the fragile bone structure needed for low wing loading. Fractures of the pectoral girdles (18.6%) in Cooper's Hawks may be due to impacts while attempting to secure prey (Roth et al. 2002). Murza et al. (2000) found a lower injury incidence in American Kestrels (6%), which might be explained by the hunting strategy of kestrels. Kestrels do not use their talons to kill prey as do other raptors, but merely as extensions of their toes to hold prey and quickly damage the spinal cord with their bill (Csermely et al. 1998). We surmise the risk of the Red-tailed Hawk's foraging strategy lies between that of Cooper's Hawks and kestrels, and the frequency of injury (9%) is between the previous estimates documented for those species. Red-tailed Hawks hunt in relatively open areas which decreases the risk of impacts and fractures, but their prey is often larger and stronger than that taken by kestrels.

Our data suggest the frequency of injuries in raptorial species is relatively high. A more in depth examination of birds trapped in wintering areas may provide more data regarding healed fractures and previous injuries. Many injuries incurred by raptors may ultimately result in death (e.g., eye lesions or hallux injuries), but our data suggest that many external injuries are not as detrimental as might be expected.

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Spring Temperatures in Relation to Laying Dates and Clutch Size of the Blue Tit (*Parus caeruleus*) in Croatia

Zdravko Dolenec[1]

ABSTRACT.—This study was based on spring temperatures, laying dates, and clutch size of the first nesting attempt of the Blue Tit (*Parus caeruleus*) from 1982 to 2004 in Hrvatsko Zagorje rural area (46° 00′ N, 15° 55′ E), Croatia. The results suggest that timing of breeding of the Blue Tit is influenced by spring air temperatures. There was a significant correlation between spring temperature and years, consistent with a global warming trend. The date of clutch initiation in the Blue Tit population studied did not decrease over a 23-year period. Correlations between spring temperatures and clutch size, and year and clutch size were not significant. *Received 13 January 2006. Accepted 7 October 2006.*

Several authors have discussed use of birds (and other organisms) as sensitive biomonitors for climate change (e.g., Winkler et al. 2002, Parmesan and Yohe 2003). Climate change affects bird migration (e.g., Sokolov and Payevsky 1998, Dolenec 2003) and breeding phenology (e.g., Dunn and Winkler 1999, Sergio 2003), and it is likely that these trends are caused by global warming. However, it is necessary to conduct relevant studies on more species in extensive areas to confirm changes are occurring (Koike and Higuchi 2002).

I investigated the long-term variation in laying dates and clutch sizes of the Blue Tit (*Parus caeruleus caeruleus*) (Vaurie 1959) to examine breeding phenology in relation to spring temperatures. The Blue Tit is a common and sedentary species in northwestern Croatia.

STUDY AREA AND METHODS

This study was conducted during the breeding seasons of 1982 to 2004 in deciduous forest (45° 50′ to 46° 00′ N, 15° 50′ to 16° 00′ E) in the Hrvatsko Zagorje area of northwestern Croatia. All records used in this study were from nest boxes. The internal dimensions of the nest boxes were 120 × 120 × 230 mm, and the front section had a 29-mm diameter hole. All nest boxes had a sliding top to enable observers to monitor nesting. Only clutches from pairs that bred in nest boxes were included. Nest boxes were placed 50 m apart on deciduous trees (2.5–5 m above the ground) and were inspected every 1–5 days. The dominant tree species were oak (*Quercus robur*) and hornbeam (*Carpinus betulus*); other tree species that occurred in low proportion included: common maple (*Acer campestre*), ash (*Fraxinus angustifolia*), and common elm (*Ulmus minor*). The number of nests in the sample varied from year to year (range = 19 to 39 nests per year, mean = 30.4 nests per year). Blue Tits in this area rear only one brood per year. Renest clutches due to nesting failure were not included.

Spring air temperature was calculated as the mean of February, March, and April temperatures. Mean (± SD) monthly Mokrice air temperatures for February, March, and April (1982 to 2004) were provided by the Meteorological Office in Zagreb (Feb, mean = 1.7 ± 3.12° C, range = −4.2 to 6.1° C; Mar, mean = 6.1 ± 2.26° C, range = 0.9 to 10.2° C; Apr, mean = 10.6 ± 1.35° C, range = 7.9 to 13.8 °C).

RESULTS

I calculated Pearson's correlation coefficient between clutch initiation and mean spring temperatures to examine long-term trends in egg-laying dates. There was a significant correlation between timing of clutch initiation and the mean spring temperature ($r = -0.483$, $P = 0.019$, $n = 23$; Fig. 1). The relationship between mean laying date (y) and spring air temperatures (x) was $y = 49.9 - 2.09x$, indicating that laying dates decreased by 2.09 days per 1° C. There was no significant correlation between mean clutch initia-

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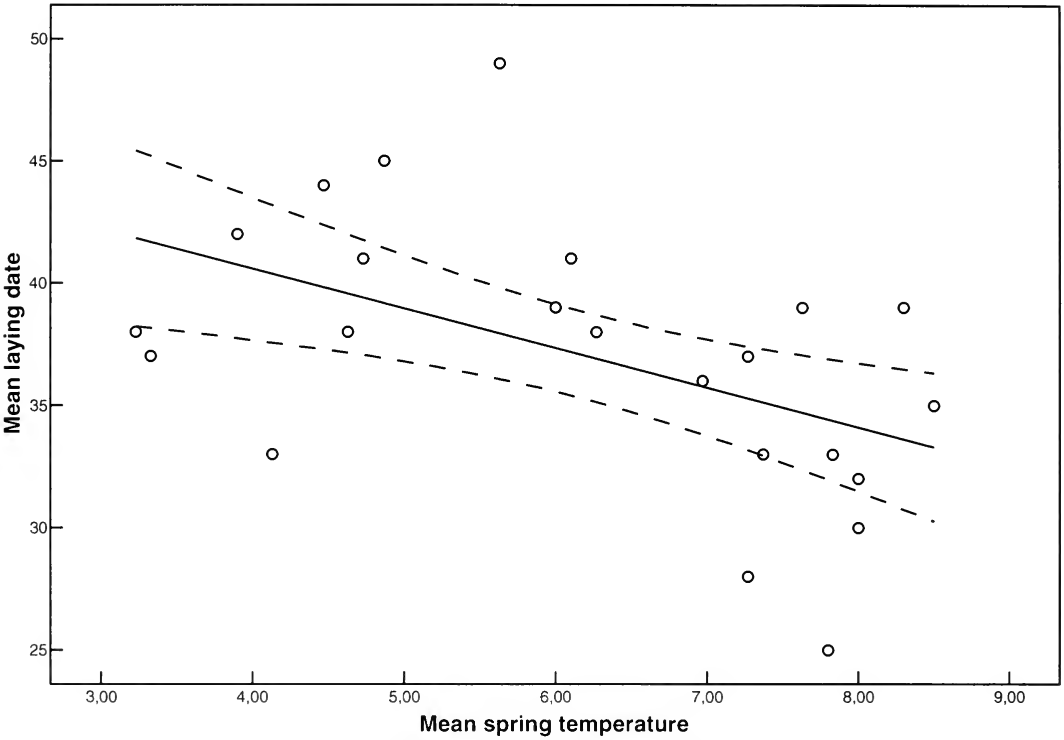

FIG. 1. Correlation between laying date and spring temperature for Blue Tits in Mokrice, Croatia, 1982 to 2004 (Pearson's correlation coefficient: $r = -0.483$, $P = 0.019$, $n = 23$; $y = 49.9 - 2.09x$; for date, 1 Mar is day 1) (dashed lines represent borders of 95% confidence interval).

tion date and the entire research period (from 1982 to 2004; $r = -0.075$, $P = 0.734$, $n = 23$). The correlation between mean spring temperatures and year was significant ($r = 0.417$, $P = 0.048$, $n = 23$; Fig. 2). The relationship between spring air temperatures and year ($y = -203.08 + 0.11x$) indicates that spring air temperatures are rising 0.11° C per year. The correlation between spring temperatures and clutch size was not significant ($r = 0.306$, $P = 0.156$, $n = 23$). Thus, clutch size in the Blue Tit population studied did not advance over a 23-year period ($r = 0.361$, $P = 0.091$, $n = 23$).

DISCUSSION

My results suggest that timing of breeding of the Blue Tit is influenced by spring air temperatures. It has been shown that many bird species are egg laying progressively earlier in response to global warming. For example, from 1971 to 1995, significant trends toward earlier laying dates were found in 20 bird species in the United Kingdom (Crick et al. 1997). This pattern is confirmed by long-term studies of bird populations (e.g., McCleery and Perrins 1998). According to Crick et al. (1997), earlier nesting could be beneficial if juvenile survival is significantly enhanced before winter; conversely, birds may be adversely affected if they become unsynchronized with the phenology of their food. Ornithological studies have provided some of the best examples regarding the impacts of recent climate change on wildlife from around the world (Crick and Sparks 1999, Crick 2004). One potential problem with correlation studies is there may be a publication bias towards reporting advances in timing of breeding because of the general expectation that climate change should cause advancements, rather than publication of a lack of trends, or even delays in nesting (Both et al. 2004).

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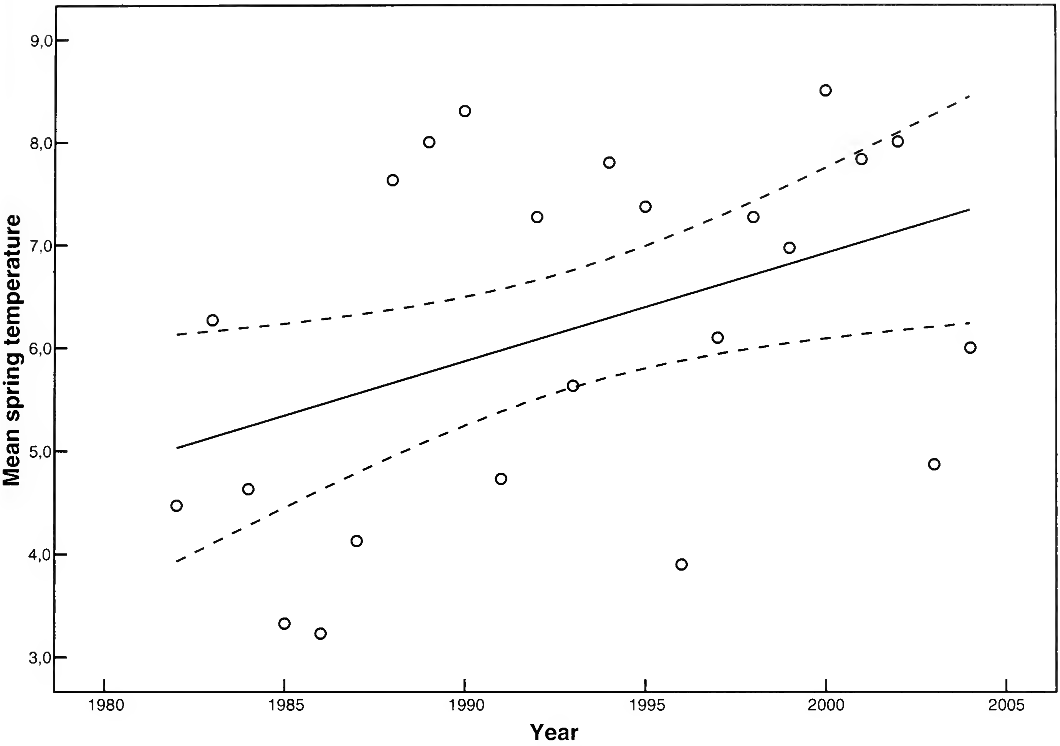

FIG. 2. Correlation between spring temperatures and year for Blue Tits in Mokrice, Croatia, 1982 to 2004 (Pearson's correlation coefficient: $r = 0.417$, $P = 0.048$, $n = 23$; $y = -203.08 + 0.11x$) (dashed lines represent borders of 95% confidence interval).

improve this manuscript. I also thank the Meteorological Office in Zagreb for providing the spring temperature data.

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Mother-son Parental Care in Horned Larks

Alaine F. Camfield,[1,3] Alana J. Clason,[1] and Kathy Martin[1,2]

ABSTRACT.—We report the first known observation of mother-son parental care and potential inbreeding in Horned Larks (*Eremophila alpestris*) near Smithers, British Columbia, Canada. The nest was found with four nestlings and was attended by a female and her son from the previous year. The nestlings appeared healthy, were above average mass, and fledged successfully. The high return rates of adult and juvenile Horned Larks at our study site may have facilitated this social pairing by close relatives. The possibility the son was a helper at the nest is discussed. *Received 10 March 2006. Accepted 5 September 2006.*

Inbreeding depression in birds has been reported to affect a number of traits including hatching success (Bensch et al. 1994, Spottiswoode and Moller 2003), nestling mortality (Greenwood et al. 1978), survival (Keller 1998), and recruitment (Bulmer 1973). Pair formation among close relatives is generally thought to be rare (Pusey 1987) due to the deleterious effects of inbreeding and behavioral mechanisms such as natal dispersal that appear to have evolved to reduce the chances of inbreeding (Weatherhead and Forbes 1994). However, rates of inbreeding may be under reported because estimating inbreeding requires long-term studies of marked individuals (Keller 1998). Indeed, new evidence suggests that inbreeding may be more prevalent than previously thought (Keller and Waller 2002). We report the first known instance of mother-son parental care and potential inbreeding in Horned Larks (*Eremophila alpestris*).

OBSERVATIONS

We observed a case of a mother and son social pair of Horned Larks providing parental care in June 2005 on Hudson Bay Mountain near Smithers, British Columbia, Canada (52° N, 127° W). The study site is approximately 4 km^2 and there are typically 40–50 Horned Lark pairs breeding at the site. The population of Horned Larks in the region is not well defined; however, neighboring mountain ranges (>25 km distant) likely support breeding populations. Each year we locate and monitor Horned Lark nests, and band adults and nestlings with individual color band combinations. The female in this case was banded as a breeding adult in 2004 and the male was banded as one of her nestlings in 2004. The female's nest was found in 2004 while she was incubating, and she subsequently fed and successfully fledged five nestlings, one of which returned to the study area in 2005. The female's mate from 2004 returned in 2005; however, she formed a social pair with her son from 2004 and her previous mate paired with a new female (the male was first seen on 16 May 2005 together with his unbanded mate). The son was first seen on 24 May 2005 on the same territory where the nest was found; the female was not seen until the nest was found. On 19 June 2005 we found a nest with four nestlings (7–8 days old) that were actively being fed by the mother-son pair; the nest fledged on 21–22 June 2005. The male and female at this nest were captured and their band numbers read to confirm their identity. The male and female of the mother-son pair were observed provisioning young at the nest during four nest visits totaling approximately 4 hrs. Both adults were equal participants in provisioning nestlings and no other individuals were seen around the nest.

The female's 2004 mate retained his 2004 territory which was >500 m from the mother-son pair. He had two nests with his new mate in 2005; both clutches were depredated. This male was not seen with the female or on the territory of the mother-son pair in 2005.

The clutch size (four young) of the mother-

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son nest was within the range for the population in 2005 (n = 57, mean [± SE] 3.7 ± 0.1, range 2–5). The nestlings appeared healthy; they were alert, active, and showed no signs of ectoparasites. They were weighed at 8–9 days of age and had slightly larger mass (n = 4, 24.2 ± 1.4 g, range 21–27.5) than nestlings of the same age in other nests (n = 20, 22.1 ± 0.56 g, range 16.5–26.5).

DISCUSSION

Birds often use breeding success in the previous year as a cue to change or remain with a mate (Dubois and Cezilly 2002). In this case, the female Horned Lark switched mates and apparently paired with her son even though she successfully fledged young in the previous year with her previous mate. It is possible that she left her previous mate as a result of coercion; however, in songbirds females typically initiate mate switching (Grant and Grant 1987, Linden 1991, Dhondt and Adriaensen 1994, Blondel et al. 2000).

There are several possible explanations for this observation provided the nest was the result of mother-son inbreeding. First, if there are no mechanisms by which closely related Horned Larks recognize each other, mother-son pairings may be as common as expected under random mating. We observed a return rate of 80% of banded adults in our study and in 2005, 25% of banded juveniles from 2004 returned (AFC, unpubl. data). The high return rates of both adults and juveniles may have facilitated a social pairing by close relatives. Second, the costs of avoiding inbreeding or failing to reproduce may outweigh the costs of inbreeding. Finally, females may have access to extra-pair copulations which would negate the effects of pairing with a close relative. However, long-term studies of color-marked Horned Lark populations are lacking and rates of extra-pair copulation are unknown (Beason 1995).

This observation may possibly be an example of helping at the nest. Helpers at the nest are birds that aid a breeding individual that is not its mate and/or feed nestlings or other birds that are not their offspring or mate (Skutch 1961). Only one instance of helping has been reported for Horned Larks (Beason 1984). His observation occurred when fledglings intruded onto a nearby territory and were fed by adults other than their own parents. This may have been an example of helping; however, it is more likely to have been the result of the adults mistaking intruding fledglings as their own offspring. It is possible for our observation of mother-son offspring feeding that the son was a helper at the nest. However, given the son was observed on the same territory a month before the nest was found, the female was not seen with another male, and no birds other than the mother-son pair were seen tending the nest, this scenario seems unlikely. It is also possible the male from 2004 mated polygynously with the female at this nest and his new mate in 2005. However, this scenario is unlikely since the two territories were more than 500 m apart, were separated by several territories, the male and female were not seen together, and the male did not feed at this nest even after both his 2005 nests failed.

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Interspecific Interactions between Marsh-dwelling *Ammodramus* Sparrows at a Migration Stopover

Alexis F. L. A. Powell[1,2,3] and Arpad S. Nyari[1]

ABSTRACT.—The social behaviors of Le Conte's (*Ammodramus leconteii*) and Nelson's Sharp-tailed (*A. nelsoni*) sparrows are poorly documented, as are their interactions with one another, even in the prairie marshes they share during the breeding season. We report the regular coincident presence and similar habitat associations of these species at a fall migration stopover, the Baker University Wetlands, near Lawrence, Kansas, over an 11-year period, and describe social behaviors (several previously unrecorded) at the site, including an aggressive interspecific encounter.

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Le Conte's Sparrow (*Ammodramus leconteii*) and Nelson's Sharp-tailed Sparrow (*A. nelsoni*) are physically similar, closely related species that breed syntopically in the marshy grasslands and bogs of Canada's prairie provinces and the extreme northcentral United States (Murray 1969). Little is known about these species' interactions on the breeding grounds despite their close evolutionary relationship and intimate ecological association, and nothing has been reported of their behavior toward one another during migration (Greenlaw and Rising 1994, Lowther 2005). Here, we report an instance of interspecific aggression at a migration stopover.

Shortly after sunrise on 21 October 2004, while photographing Le Conte's Sparrows at the Baker University Wetlands, near Lawrence, Kansas (38° 55′ N, 95° 14′ W), we encountered a Nelson's Sharp-tailed Sparrow moving through the vegetation in our direction. It paused, perched on the fallen-over dried stem of a sunflower (*Helianthus* sp.). A few seconds later, a Le Conte's Sparrow landed ~60 cm from the sharp-tail and quickly clambered down the stem toward it, initiating a confrontation that ended after ~5 sec when the sharp-tailed sparrow flew ~10 m away. We did not have the presence of mind to recall specifics of wing flapping and vocalizations during the fight except to note that they occurred; some rising raspy cries may have been equivalent to the "scream" of the Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*; Greenlaw and Rising 1994). One of us (AFLAP) took two photographs during the incident. The first (Fig. 1) shows both individuals with heads forward and beaks gaping. The second (Fig. 2), taken just before the sharp-tailed sparrow flew away, shows the Le Conte's Sparrow, having moved much closer to the sharp-tailed sparrow, with neck fully extended and beak open as if to deliver a bite. These behaviors, previously unreported for these

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FIG. 1. Nelson's Sharp-tailed Sparrow (left) and Le Conte's Sparrow performing head-forward and gaping threat displays to one another.

species, are known threat displays in other passerines; Post and Greenlaw (1975:477) note that captive Saltmarsh Sharp-tailed and Seaside (*A. maritimus*) sparrows "commonly give" and "often continue the head forward threat into an active attack, pulling the tail or body plumage of an opponent. Both species use the display against each other."

This incident is the only time we witnessed direct physical interaction between Le Conte's

FIG. 2. Nelson's Sharp-tailed Sparrow (left) just prior to flying and Le Conte's Sparrow.

and Nelson's Sharp-tailed sparrows even though we spent several hours each fall, 1994–2004, watching these species at the Baker University Wetlands. In most years, we found Le Conte's Sparrow throughout October (records 3 Oct to 6 Nov for migrants; single birds seen later perhaps being winter residents) with peak numbers of ~60 individuals per morning during the third week of October. Nelson's Sharp-tailed Sparrow was much less numerous, but timing of occurrence (records 3 Oct to 4 Nov) and peak abundance of 3–6 individuals per morning, were the same. Both species occupied stands of prairie cordgrass (*Spartina pectinata*) in a matrix of shorter annual forbs and spikerush (*Eleocharis* sp.). We routinely observed individuals of both species ascending, perching and, in the case of Nelson's Sharp-tailed Sparrow, foraging on cordgrass seeds and adult crane flies (Tipulidae) near the tops of cordgrass stems (~150+ cm height). We have not had comparable experiences in spring, having only sporadically found small numbers of Le Conte's Sparrows (~3 in a morning; records 28 Mar to 8 May), and entirely missed Nelson's Sharp-tailed Sparrow during its passage in mid May to early June (Murray 1969, Greenlaw and Rising 1994).

These species often occurred in the same overall areas and habitat on the same days in the fall, but we rarely found them together (within ~10 m of one another) leading us to suspect that Nelson's Sharp-tailed Sparrow avoids the generally more territorial and less social Le Conte's Sparrow. Le Conte's Sparrows are territorial on their breeding grounds, whereas syntopic Nelson's Sharp-tailed Sparrows are not. Murray (1969) noted that Le Conte's Sparrows at times chased or supplanted (on a perch) Nelson's Sharp-tailed Sparrows, although he did not report physical fights between these species or among conspecifics. The ranges of these species overlap in winter, but Le Conte's Sparrow occurs throughout much of the southeastern United States (especially east Texas), whereas Nelson's Sharp-tailed Sparrow is restricted to the Gulf and southern Atlantic coasts (Murray 1969, Greenlaw and Rising 1994). Le Conte's Sparrows reportedly maintain individual wintering territories (Grzybowski 1983), but we note they frequently land together after being flushed, and cluster loosely (e.g., eight individuals in a ~9 m^2 cordgrass patch) when disturbed, such as after being flushed repeatedly or in response to spishing.

We have not observed Nelson's Sharp-tailed Sparrows joining Le Conte's Sparrow congregations, but we have on several occasions seen two individuals closely associating with one another. One of us (AFLAP, on 27 Oct 2000) saw two Nelson's Sharp-tailed Sparrows stay within 1 m of one another for most of ~40 min, during which time they moved around (~100 m), remaining above the dense leafy portion of the grasses in the area by fluttering or clambering from one cordgrass stem, sunflower stalk, or other dried forb to another. They shared a common perch for almost half that time: ~12 min on a dried forb stem while stripping seeds from cordgrass heads that had become twisted around it, ~8 min doing the same at a location ~10 m from the first, and several minutes together in a small tree. On five occasions, one or the other gave a vocalization matching the "cee lisp" contact call used by Saltmarsh Sharp-tailed Sparrows in the loose foraging groups they form post-breeding and during migration; this vocalization has not been previously documented in Nelson's Sharp-tailed Sparrow (Greenlaw and Rising 1994), but we have watched individuals give this same call during other of our encounters with the species.

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Unusual Barn Swallow Nest Placement in Southeastern Oregon

Lucas J. Redmond[1,2] and Michael T. Murphy[1]

ABSTRACT.—Barn Swallows (*Hirundo rustica*) historically nested along cliffs, in caves, and in other natural situations. Currently, nearly all reported nests of this species are on walls and beams of bridges, buildings, and other human-derived structures. Both natural and man-made nest sites typically share one thing in common: a horizontal surface for nest attachment. We describe a Barn Swallow nest that was constructed on a branch overhanging a river in southeastern Oregon. This is the first documented occurrence of this behavior by Barn Swallows and we believe it to be the result of high competition for a limited number of suitable nest sites in the study area. *Received 23 February 2006. Accepted 1 August 2006.*

The Barn Swallow (*Hirundo rustica*) is perhaps the most well-studied species of swallow in the world. It breeds throughout the northern hemisphere, including much of North America. Historically this species nested in caves and on cliffs but now nests primarily on artificial structures (i.e., eaves, bridges, etc.). A search of the literature regarding nest placement of this species indicated that nests away from vertical structures (both natural and artificial) are rarely reported, if at all (Speich et al. 1986). Nest architecture is perceived to be a relatively fixed trait with an underlying genetic basis, as studies have shown its usefulness in phylogenetic analyses (Winkler and Sheldon 1993, Zyskowski and Prum 1999). We report on observations of two atypically constructed nests of Barn Swallows in southeastern Oregon.

OBSERVATIONS

On 17 June 2004, MTM found a Barn Swallow nest being built in a willow tree (*Salix* sp.) along the Donner und Blitzen River at Malheur National Wildlife Refuge near Frenchglen, Oregon. The Central Patrol Road (CPR) parallels the stretch of river where the nest was located. Trees line much of the narrow bank between the river and road, and the nest tree (42.91713° N, 118.87425° W) was approximately 3 m from the west shoulder of the road and 10.8 km north of the southern end of the CPR. Coordinates of the nest were documented with a Garmin GPS 72 receiver.

MTM's attention was drawn to the half-built nest because its position suggested that of an Eastern Kingbird (*Tyrannus tyrannus*) (the focus of another study). Recognition that it was constructed of mud prompted further attention, and within minutes a Barn Swallow alighted upon the nest and deposited mud along its rim. The nest was attached to the end of a dead limb hanging over the river. It was approximately 0.25 m above the water's surface and made entirely of small, individual "globules" of mud of a nearly perfectly circular shape attached to a single, downward projecting limb that measured 9.5 mm in diameter. The limb provided a narrow attachment site for the base and one side of the nest. LJR documented the finding with several photographs (Fig. 1).

We checked the nest every 3–4 days to ascertain its outcome. On 24 and 25 June there were five eggs in the nest and the female was incubating the clutch on all visits. On 28 June a storm accompanied by high winds moved through the area and on 29 June the entire nest was gone. We presume that it was blown from the tree.

On 9 July, LJR located another nest in the same tree in exactly the same position as the first nest. The nest appeared to be complete and contained no eggs, but otherwise appeared to be constructed identically to the first nest (i.e., round, made entirely of small mud globules). On 12 July, the nest held three eggs and, on 15 July, a Barn Swallow was on the nest incubating five eggs indicating that laying began on 10 July and concluded on 14 July. On 20 July, no eggs remained in the nest, but

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FIG. 1. Barn Swallow nest constructed in a willow tree over the Donner und Blitzen River, 17 June 2004, Malheur National Wildlife Refuge, Oregon.

it was intact, suggesting it was probably depredated by an avian predator. On 24 July, LJR removed the nest and the portion of branch to which it was attached. It has been deposited in the Museum of Vertebrate Zoology at Portland State University (Catalog #B1549).

DISCUSSION

The abundance of Barn Swallows most likely increased with arrival of European settlers due to increased availability of suitable nest sites. The nest we describe was in southeastern Oregon where densities of humans (<1 person/km^2) and buildings are extremely low. Thus, Barn Swallows may rely more heavily on natural nesting substrates. One of the few known colonies of naturally nesting Barn Swallows (Malheur Cave) occurs in the same county (Harney) (Speich et al. 1986). Artificial substrates are not completely lacking in the vicinity of the nests that we described; however, competition for these sites may be high. The nearest artificial nesting substrate (a small shed) was approximately 5.6 km north of the described nests. A bridge formerly crossing the Donner und Blitzen River (known locally as Five Mile Bridge) approximately 2 km upstream (south) of the nest was removed by refuge personnel in early spring 2004. A large culvert and bridge ~5.5 km south and ~6.7 km north of the site, respectively, of the tree-nesting Barn Swallows offered potential nest sites, but medium-sized (30–50 pairs) colonies of Cliff Swallows (*Petrochelidon pyrrhonota*) occupied both sites. Rocky buttes in the area also offer possible nest sites, but most are at considerable distances (≥3–4 km) from the river in dry, shrub-steppe habitat. One butte, within 100 m of the river, is ~8 km distant but is occupied by a Cliff Swallow colony.

Our research at this site (daily surveys along the same stretch of river between late May and late July in 2002 and 2003) yielded frequent observations of Barn Swallows, despite the apparent scarcity of suitable nest sites. The area also provides exceptional breeding opportunities for other swallow species and supports large breeding populations of Cliff Swallow, Northern Rough-winged

Swallow (*Stelgidopteryx serripennis*), Bank Swallow (*Riparia riparia*), and, where nest boxes are provided, Tree Swallows (*Tachycineta bicolor*). Violet-green Swallows (*T. thalassina*) are common at higher elevations on nearby Steens Mountain and during cold weather they descend to forage along the river. Hence, food must be abundant for aerial foragers and we suspect that availability of aerial insects attracted the Barn Swallows to the area, despite the shortage of nest sites.

Our observations demonstrate that Barn Swallows possess the behavioral flexibility to build nests in a manner that is entirely outside their expected repertoire. Mayr and Bond (1943) were the first to construct a phylogeny of swallows based mostly on nesting habits, which was later supported by a molecular phylogenetic analysis (Sheldon and Winkler 1993). However, the two Barn Swallow nests that we observed were outside that expected for this genus. Cliff Swallows also construct nests in atypical manners such as cavity excavation (Gaunt and Gaunt 1967) and in trees (Dawson 1923, Garrett 2002). Thus, there may be some amount of inherent plasticity in nest building behavior within the *Hirundo* clade (Winkler and Sheldon 1993). Researchers studying Barn Swallows should identify the extent to which non-traditional nest sites are used by this species.

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Mortality at a Night Roost of Great-tailed Grackles and European Starlings During a Spring Hail Storm

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ABSTRACT.—We report on mortality caused by an evening hailstorm to a night-time roost of Great-tailed Grackles (*Quiscalus mexicanus*) and European Starlings (*Sturnus vulgaris*) in Austin, Texas. The hailstorm was of short duration (6 min), and hail stones were not too large (most <20 mm in diameter). Approximately 7% of female grackles, 12% of male grackles, and 26% of starlings died. Greater mortality in male grackles suggests that preferred roost locations were more exposed to hail. *Received 28 November 2005. Accepted 3 September 2006.*

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Bird mortality due to hailstorms has been documented on only a few occasions (Smith and Webster 1955, Roth 1976, Beedy and Hamilton 1977, Higgins and Johnson 1978, Heflebower and Klett 1980, Martin et al. 1998, Schweitzer and Leslie 2000), even though mortality can be substantial (Smith and Webster 1955). In this note, we present the effects of a hail storm on a night-time roost of Great-tailed Grackles (*Quiscalus mexicanus*) and European Starlings (*Sturnus vulgaris*) in Austin, Texas.

METHODS

On 25 March 2005 between 2115 and 2130 hrs CST, a thunderstorm of short duration passed through Austin (Travis County), Texas. The storm was notable as it included a downfall of hail that lasted ~6 min. The storm passed directly over DWH's home (8505 Dorotha Ct., Austin) and he observed hail 5–20 mm in diameter, although hail up to 40 mm was reported in other areas. The hail knocked many small branches (<5 mm diameter) and leaves from trees and shrubs, damaged the fabric tops of some automobiles, and broke a few windows in residences and automobiles.

The following morning, 26 March 2005, between 0730 and 1000 hrs, we censused areas surrounding Highland Mall (6001 Airport Blvd., Austin) for dead and injured birds. Highland Mall is ~7 km from DWH's residence in the direction the storm was moving (southeast). Trees surrounding Highland Mall were known to have night-time roosts of Great-tailed Grackles and European Starlings (DWH, pers. obs.).

We estimated the number of birds killed or injured by the hailstorm by censusing seven vegetated areas, each of which contained at least two trees suitable for night-time roosts. These areas were chosen haphazardly and the only requirement was that they had well-defined borders so we could revisit them in the evening. The seven areas varied in length from 25 to 125 m, and contained up to 15 roost trees.

The census involved counting the number of dead and stunned individuals (by gender for grackles) present on the ground or in vegetation up to 2 m in height. Birds present in trees were not counted. Heavy ground cover (a dense hedge) in area 7 was surveyed without intrusion to reduce the likelihood that injured birds would flee onto the adjacent roadway.

We estimated flock density before the hailstorm by assuming that all uninjured birds would return to their usual roost in the evening. We censused roosting birds by counting individuals in trees during the last 45 min of daylight (1830–1915 hrs) the next day, 26 March 2005, following the hail storm. All birds were counted for areas 5–7. We had to estimate the number of roosting birds for areas 1–4 because light levels were rapidly decreasing, making counting difficult. We carefully counted the birds in three oak (*Quercus* spp.) trees in transect 1 and calculated an average. We used this average to estimate the total number of birds in areas 1–4. The trees in all four of these areas were oaks of similar size (presumably planted when Highland Mall was built in the early 1970s). The areas had similar ground vegetation (grass with a few flowerbeds).

RESULTS

Injured individuals varied greatly in their condition. Some (~50%) had sustained relatively minor injuries and were able to flee when approached, while others were more severely injured and could be approached closely. If we presume that most injured birds, regardless of severity of injury, were unlikely to recover, overall mortality was 12% in male Great-tailed Grackles, 7% in female Great-tailed Grackles, and 26% for European Starlings (Table 1). Male Great-tailed Grackles were more likely to be dead or injured than females (Fisher's exact test, $P < 0.001$). European Starlings were more likely to be dead or injured than Great-tailed Grackles (Fisher's exact test, $P < 0.001$).

DISCUSSION

The hailstorm of 25 March 2005, although relatively short in duration (~6 min) with relatively small hail stones (<20 mm in diameter), caused substantial mortality at the night-time roost of Great-tailed Grackles and European Starlings at Highland Mall. Starlings were particularly affected by the storm, perhaps due to their smaller body size. Male grackles survived more poorly than females, possibly due to the position in the tree crown they occupied. We observed that female

TABLE 1. Dead and injured birds at seven areas surrounding Highland Mall, Austin Texas, 26 March 2005. Areas 1, 3, 4, 5, and 6 each also contained one dead White-winged Dove (*Zenaida asiatica*). Area 5 contained one injured Purple Martin (*Progne subis*). Areas 6 and 7 each contained one injured White-winged Dove. Area 7 contained one dead Cedar Waxwing (*Bombicilla cedrorum*). Total abundances at the evening census were counted for areas 5–7 and were estimated for areas 1–4 by carefully counting birds present in three oak trees in area 1 and then extrapolating. GTG = Great-tailed Grackle. ES = European Starling.

	Dead			Stunned			Evening census		
Census area	GTG male	GTG female	ES	GTG male	GTG female	ES	GTG male	GTG female	ES
1	13	15	21	5	3	3	173[a]	510[a]	25[a]
2	14	13	18	7	12	6	173[a]	510[a]	25[a]
3	14	19	22	6	5	5	207[a]	612[a]	30[a]
4	8	8	2	1	2	1	69[a]	204[a]	10[a]
5	9	17	3	3	0	0	13	48	132
6	10	19	5	1	6	0	51	59	36
7	10	40	11	3	6	0	77	176	16
Totals	78	131	82	26	34	15	763	2,119	274

[a] Estimated.

grackles at the evening census roosted lower in the crown than males, which aggressively sought uppermost positions. Males placed themselves in a position that was more exposed and more susceptible to hail injury. Males sought a higher position, perhaps because it was more protected from predators and from fecal precipitation (Yom Tov 1979, Burger 1981, Weatherhead 1983). Our mortality data suggest this preferred position had a cost during the hail storm.

We may have underestimated hail mortality. First, during the morning census, birds perched in trees were not counted even though some birds may have been injured (one male Great-tailed Grackle flew from a tree and crashed into a sign, indicating it had sustained an injury). Second, to avoid stressing injured birds, heavy cover in area 7 was not searched thoroughly and some dead or injured birds may have been overlooked. Third, some injured birds may have moved from the census areas prior to the morning census.

We may also have overestimated hail mortality. First, some birds may not have returned to the Highland Mall roost on the evening following the hailstorm. Second, some birds may have arrived at the roost after it was too dark for us to count them. Third, some birds may have been overlooked in the evening census: starlings tended to aggregate towards the center of a roost tree and were more difficult to count than grackles.

The possible inaccuracies of our estimates underscore the difficulty of obtaining these data. Hail storms are unpredictable both spatially and temporally, and mortality surveys must be done soon thereafter. Our study was in an area where dead and injured birds could be easily found and population size could be relatively easily estimated. Obtaining estimates of the impact of hail storms on other species, especially those in rural areas, would be much more difficult. Many such areas are hard to access, population size is not easy to estimate, and the vast amount of plant material knocked down buries small birds, making them difficult or impossible to find.

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First Record of Bronzed Cowbird (*Molothrus aeneus*) Parasitism of the Common Bush-tanager (*Chlorospingus ophthalmicus*)

Fernando González-García[1]

ABSTRACT.—I report the first record of Bronzed Cowbird (*Molothrus aeneus*) parasitism of the Common Bush-tanager (*Chlorospingus ophthalmicus*). This represents the 97th known host for this cowbird species and the 10th known host from the Family Thraupidae. This record is based on feeding behavior observations and vocalizations recorded in Xalapa, Veracruz, Mexico. *Received 9 February 2006. Accepted 18 July 2006.*

Brood parasitic cowbirds (*Molothrus* spp.) differ greatly in the number of hosts. Bronzed (*M. aeneus*), Brown-headed (*M. ater*), Shiny (*M. bonariensis*), and Screaming (*M. rufoaxillaris*) cowbirds are reported to have parasitized between 10 and 200 hosts (Fraga 2005, Ortega et al. 2005, Peer et al. 2005). The Bronzed Cowbird is a generalist brood parasite known to have parasitized ~100 host species (Sealy et al. 1997, Peer et al. 2005), but this species has been little studied and new data on its host use are especially valuable (Carter 1986, Peer et al. 2005). The Common Bush-tanager (*Chlorospingus ophthalmicus*) has not been reported as a Bronzed Cowbird host (Lowther 2005). I report here observations indicating this species successfully reared a Bronzed Cowbird.

The Common Bush-tanager is a small tanager and a common resident of montane tropical forest, even in remnant strips of humid evergreen forest and edge. It ranges from Mexico to Bolivia and northwestern Argentina (Skutch 1967, Stiles and Skutch 1989, Howell and Webb 1995). The Common Bush-tanager in Mexico inhabits areas from 1,000 to 3,500 m elevation (Howell and Webb 1995). The female builds an open cup nest with rootlets, grass, moss, and epiphytes at mid-levels in trees, or hidden in undergrowth on banks. Clutch size is 2–3 white eggs flecked with reddish browns and grays that are incubated by the female alone (Skutch 1967, Stiles and Skutch 1989, Howell and Webb 1995). The Common Bush-tanager is a common resident in the study site and in other Mexican cloud forests, but there are no records of brood parasitism of this species by Bronzed Cowbirds (Peer et al. 2005).

STUDY AREA

The observation site was in a remnant of tropical montane cloud forest in Francisco X. Clavijero Park (18° 30′ 47.5″ N, 96° 56′ 33.3″ W; 1,310 m), near the Instituto de Ecología,

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A.C. This natural protected area is 2.5 km south of the city of Xalapa, Veracruz, Mexico encompassing an area of 55 ha. It receives 1,517 mm of rain per year and the mean annual temperature is 18° C. The topography of the area is irregular with steep slopes (40%). The mean canopy height is 24.6 ± 1.1 m (Williams-Linera 1993, 2002). Canopy and understory dominant trees included *Carpinus caroliniana*, *Liquidambar styraciflua*, *Quercus xalapensis*, *Q. leiophylla*, *Q. germana*, *Clethra mexicana*, *Turpinia insignis*, *Cinamomun effusum*, *Eugenia xalapensis*, *Lonchocarpus* sp., *Meliosma alba*, *Ilex tolucana*, and *Oreopanax xalapensis* (Williams-Linera 1993, 2002).

OBSERVATIONS

My observations of Bronzed Cowbirds and Common Bush-tanagers were on 14, 24, and 25 August 2001. I was attracted to the fledged juvenile Bronzed Cowbird accompanied by a single Common Bush-tanager by its loud vocalizations. On 14 August, I observed and tape recorded this pair for 15 min (recordings deposited in the Mexican Bird Sound Library, GOGF01-156-017, 018). The cowbird fledgling was attended by only one tanager and was fed four times, apparently with insects. Feedings were primarily in the middle part of an oak (*Quercus* sp.) tree. The tanager moved vigorously on the oak branches uttering calls and searching for food, and the cowbird called loudly and continuously. The cowbird's calls were louder when it was fed by the tanager. The cowbird perched in the oak, begging for food with its yellowish bill open, and moving and vibrating its wings while the tanager searched for food. The cowbird fledgling's size was similar to that of an adult cowbird, but with paler and browner plumage without sheen and with brown eyes. On 24 and 25 August, I saw the tanager and cowbird fledgling again in the same oak tree performing similar behaviors.

DISCUSSION

The Bronzed Cowbird breeds in Mexico from sea level to at least 3,000 m (Howell and Webb 1995). There are no census data on Bronzed Cowbirds for the study site but single individuals are seen infrequently at irregular intervals. The species is more frequent in open and semi-open areas although it does not form large flocks. I have also seen cowbird fledglings at 1,400 m using Rusty Sparrow (*Aimophila rufescens*) as hosts (a known host species; Lowther 2005). The Rusty Sparrow is probably a common host of *Molothrus aeneus* in Veracruz (Friedmann 1933, Lowther 2005) as it is a common resident species in Natura and Francisco X. Clavijero parks. The Common Bush-tanager is a common species in the cloud forest of this study site and is probably regularly parasitized.

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Once Upon a Time in American Ornithology

The 5th edition of the AOU *Check-list of North American Birds* redefined North America to include Mexico and Central America (American Ornithologists' Union 1983: x). This change introduces a new perspective of the avian natural history of North America, and brings to the fore a little known Spanish ornithological contribution and its Aztec and Spanish collaborators.

Who among we Anglophone ornithologists recognize the name of Fray Bernardino de Sahagún or know of his great opus *Historia general de las cosas de Nueva España,* in English referred to as the *Florentine Codex.* While little known to English-only speaking ornithologists, Sahagún is revered in Mexico, where its federal government annually bestows four prestigious awards in his name.

So who was Fr. Bernardino de Sahagún and what is the *Florentine Codex*? Relatively little is known of his life. Born c. 1500 in Léon, Spain, and after being educated at the University of Salamanca and taking Franciscan vows, Fray Sahagún (Fig. 1) arrived in New Spain (Mexico) in 1529 with 19 other friars, to proselytize Catholicism among the surviving Aztecs of the Valley of Mexico. He quickly mastered Nahuatl, the missionary-devised, Spanish-alphabet written language. Additionally, he taught at the Colegio de Santa Cruz, established in Tlatelolco on 6 January 1536 to educate Aztec youths.

The expansive Valley of Mexico during the pre-Conquest (1519) period contained five large lakes perched at different elevations of which some, at times of high water, were connected. They supported extremely diversified forms of wildlife and their birds, fish, insects, and algae were important food resources.

Sahagún soon conceived that to most effectively further the missionary effort, one should broadly understand all aspects of the Aztec civilization. Consequently, he enlisted the assistance of his superior Aztec students (many learned Latin better than most Spaniards) and developed a systematized means of gathering and recording information gleaned from survivors of the Conquest. An enormous amount of information was gathered using standardized questionnaires, but it was accepted only if independently verified. In this sense, Sahagún apparently was the first European to use these two scientific principles in the New World.

In 1558 he commenced to collate the vast accumulated information from the cooperative survey and systematically organized it by books, chapters, and paragraphs according to subject matter. Sahagún's huge effort was essentially completed in Latin-Nahuatl in 1569.

Book 11, titled "Of Earthly Things", and described as "[telling] of the different animals, the birds, the fishes, and trees, and the herbs . . . " is by far the largest of the 12 volumes comprising the *Historia. . . .* Most species are described in a paragraph or two, being preceded by a small water-colored illustration.

Two copies of the original manuscript, in parallel Nahuatl and Spanish, were prepared by scribes. One of these as well as the original vanished. The second copy likewise disappeared until the early 19th century when it came to light in the Biblioteca Laurenziana Medicea in Florence, Italy. It is the source of all subsequent versions of the *Florentine Codex.*

Professor L. Bloom of the University of New Mexico visited Florence during 1938–1939 and had some 2,500 photographic negatives made of the manuscript. Further work on the project ceased with the advent of World War II. However, with peace, Professor A. J. O. Anderson of the School of American Research, Santa Fe, New Mexico and Professor C. E. Dibble of the University of Utah, Salt Lake City, decided to collaborate in producing an English-Nahuatl translation. Initially they thought that if each could devote half their time over 5 years to the endeavor they could complete the task. They were wrong, and in fact, it consumed most of their remaining lives. Eventually they wrote, "We completed our translation in 1969, four hundred years after Sahagún had completed the Nahuatl version." Their translated volumes were published intermittently by the University of Utah Press beginning in 1950. Still available, its citation is: Sahagún, B. de. 1950. *Florentine*

FIG. 1. The only known portrait of Fr. Bernardino de Sahagún, located in the Museo de Historia, Mexico City. He appears gaunt (perhaps towards the end of his 91-year life), in Franciscan habit, standing before his writing desk, quill in hand, a parchment before him, gazing pensively aside.

FIG. 2. In "hunting birds", an Aztec is gathering birds captured in vertical "bag" nets. Note their remarkable similarity to Japanese mist nets currently used by bird banders. A pelican appears in the left foreground (Sahagún 1950: Book 11, Fig. 187).

Codex: general history of the things of New Spain. (Translated and edited by A. J. O. Anderson and C. E. Dibble). Volumes 1–13. University of Utah Press, Salt Lake City, USA. (A beautiful facsimile of the Sahagún manuscript was published [Sahagún; Austin and Quitana, Editors; 1979] by the Mexican federal government).

The following is based on Book 11, "Earthly Things", of the Anderson and Dibble translation. Thirty-eight pages name approximately 140 kinds of birds, including a few duplications and occasionally the same species, differing only in plumages of different gender or age classes. Seven additional pages depict many of the species. Mexican biologist Martín del Campo identified most of those described or illustrated.

Typical descriptions provide the Aztec name in Nahuatl, appearance, habitat, food, period of presence (migrant or resident), behavioral traits, taking or capture methods (Fig. 2), edibility and sometimes, cultural or mythological attributes. A few examples follow.

Western Grebe (*Acitli* [in Nahuatl]) (page 31): "Its head is quite small, black, with a pointed . . . bill. Its eyes are like fire. It is long-necked: Its body is small and straight, small and thick; its breast very white, its back black; its legs black: they are also somewhat towards its rump. . . . It lives in the lagoon and is caught in nets."

Wood Ibis (*Quapetlaoac*) (page 32): ". . . its head is featherless, bald, bare to the neck. The sides of its head are chili-red. . . . It is long-necked. Its bill is very thick as well as cylindrical, long . . . "

Blue-winged Teal (*Metzcanauhtli*) (page 35): ". . . on its face it is decorated with white feathers like the [crescent] moon. . . . The upper coverts are pale blue; those lying in second place white, those lying in third place green, resembling quetzal feathers,"

Osprey (*Aitzquauhtli*) (page 41): "It is called *aitzquauhtli* because when it goes flying high, if it wishes to eat, from there it streaks down. When it descends, it goes whirring, it suddenly dives into the water; it seizes whatever it wishes to eat, perhaps a fish . . . "

Mourning Dove (*Vilotl*) (pages 50–51): "It is lazy. Its nest is only sticks . . . it does not drink by day, only later. And it seems constantly to weep; it makes [the sound], *uilo-o-o.*"

The 10th paragraph of Chapter 2 provides a two-page glossary of avian anatomical terms, including those for 14 feather tracts, and other body parts including the crop, gizzard, nictitating membrane, and the uropygial gland, all of whose functions the Aztecs understood.

This brief description of one of North America's most important, if not earliest, ornithological histories, should prompt others to examine this little known source, as well as help establish, tardily, Aztec ornithological knowledge to the recognition it deserves. It also credits at least one Spaniard, Fr. Sahagún, and his colleagues for preserving much of it for posterity. This summary is based upon an article titled *Sahagún's "Florentine Codex", a little known Aztecan natural history of the Valley of Mexico* (Reeves, H. M. 2006. Archives of Natural History 33: 302–321). I am indebted to the University of Utah for reproduction permissions, University of California (Berkeley) for photographic services, and the Biblioteca Laurenziana Medicea, Florence, for permission to use Sahagún materials.—HENRY M. REEVES; 22250 Boulder Crest Lane SE, Amity, Oregon 97101, USA.

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Ornithological Literature

Compiled by Mary Gustafson

HERONS. By James A. Kushlan and James A. Hancock, illustrations by David Thelwell. Oxford University Press, Oxford, U.K.: 2005: 433 pp., 18 color plates, 71 black-and-white photographs, and 62 range maps. ISBN: 0-19-854981-4, $189.50 (cloth).—This book is an addition to the *Bird Families of the World* series and contains a summary of what is know about the biology of herons. It updates the authors' previous summary, *Herons Handbook* (Hancock and Kushlan 1984, Harper & Row, New York). It is also meant to compliment *Heron Conservation* (Kushlan and Hafner 2000, Academic Press, London, U.K.), which the authors refer to as a companion volume. *Herons* consists of two parts: the first is composed of six general chapters and the second 62 species accounts. The first of the general chapters is an introduction to the herons and has sub-sections that deal with general appearance, bill, vision, head and neck, plumes and plumage, legs and feet, flight and movement, and vocalizations. The authors note that vocalizations are one of the least studied aspects of heron biology, and no sonograms are given in either the general chapters or species accounts. The second chapter deals with systematics and evolution, in which the authors incorporate the results of molecular studies and revise their assessment of the relationships of the herons of the world. Included in this revision are incorporating the night herons in subfamily Ardeinae together with the typical day herons and egrets. The other subfamilies are bitterns, tiger herons, Agami Heron (*Agamia agami*) and Boat-billed Heron (*Cochlearius cochlearius*) that is sufficiently genetically distinct to raise questions of whether it is monophyletic with the other herons. They place the Cattle Egret (previously *Bubulcus ibis*), Great Egret (previously *Egretta* or *Casmerodius alba*), and Intermediate Egret (previously *Egretta intermedia*) into genus *Ardea*. At the species level, the authors recognize a split of the Great Egret (*Ardea alba*) into a Western (*A. alba*) and Eastern Great Egret (*A. modesta*) species, accept the split of the Green Heron (*Butorides virescens*) and the Striated Heron (*B. striata*) but somewhat grudgingly retain the various populations of the Little Egret (*Egretta gularis*) group as a single species. Above the family level there remains much to be learned about the relatives of the herons. The third chapter deals with feeding ecology and includes sections on habitat, prey capture body and head postures, and a litany of foraging behaviors (e.g., Open Wing Feeding, Pirouetting, Aerial Flycatching, Feet First Diving, Baiting). The chapter also deals with commensalism and piracy, area defense, feeding dispersion, and age and foraging. Chapter four concerns nesting biology, including a discussion of the wide variety of territorial and nuptial displays (e.g., Aerial Stretch, Greeting Ceremonies, Bill Jabbing). Chapter five deals with herons and people, and chapter six with conservation. The latter deals mostly with the most threatened species of herons and with issues facing herons worldwide. It also presents two maps that show the most important areas for heron conservation around the world.

The 62 species accounts begin with various names for the species and list currently recognized subspecies. A description section includes adult and juvenile plumages, voice, and measurements. A section of field characters includes comparisons among similar appearing species. Then follow sections on systematics, range and status, habitat, foraging, breeding, population dynamics, conservation, research needs, and a summary overview. Each species account includes a range map with breeding range shown in black, and breeding/nonbreeding and nonbreeding in two shades of gray. The accounts vary in length from slightly over two pages to about a dozen, depending on available information. The first 13 plates are identification plates painted by David Thelwell and represent all 62 species. They figure, where appropriate, breeding, non-breeding, and juvenile plumages, and subspecies where the differences in plumage are significant. The extreme example is the Little Egret group where 11 birds are figured. The paintings are of uniformly high quality. Plates 13–18 are photographs of 19 species of herons and compliment the painted identification plates.

The bibliography contains more than 1,700 entries, a significant majority of which have publication dates more recent than the 1984 *Herons Handbook.* This is a valuable resource for anyone studying herons. I found the sections on Research Needs especially interesting. The authors between them have 60 years of experience with herons and are well positioned to know both what is known and what in not known about these birds. Hence, I think that this book will have considerable heuristic value. Apart from a few typos (e.g., part of one in-text reference is missing on page 87; an 'ever' should be 'even' on page 25), I have little to criticize about this book. I would like to have seen photographs of more heron species, and perhaps a table showing which foraging behaviors have been observed for each species. This book will be the standard reference on herons for several decades and the authors are congratulated on producing a well-written, remarkably jargon-free summary of our current understanding of the biology of an interesting family of birds. I highly recommend *Herons*—it is a bit pricey, but anyone interested in herons will need access to this book.—WILLIAM E. DAVIS, JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, Massachusetts; e-mail: wedavis@bu.edu

PELICANS, CORMORANTS, AND THEIR RELATIVES: THE PELECANIFORMES. By J. Bryan Nelson. Oxford University Press Inc., New York, New York. 2005: 680 pp., 12 color plates, 159 halftones, and 62 maps. ISBN: 0-19-857727-3, $174.50 (cloth).—This addition to the *Bird Families of the World* series covers a sizeable and significant group of seabirds and colonial waterbirds from six related families. Throughout the text, the author strives to merge common themes with specific information in a narrative language that helps guide the reader to a better understanding of these birds as individual species, as well as integral components of their larger families and Order. To accomplish this, the book is arranged in three major divisions. The first includes four chapters covering broad themes including evolutionary relationships and comparative breeding behavior within the Order, concepts of breeding ecology such as colonial breeding, and relationships with humans from folklore to modern conflicts with commercial aquaculture. The second division covers general family accounts including taxonomy, and summarized aspects of behavior and ecology that are omitted in later individual accounts. The third section presents the individual species accounts structured in a similar manner as the family accounts, with detailed identification, measurements, and species-specific behavior and ecology.

The book is a product of the author's considerable knowledge of sulids along with that of other experts in the field, as well as an extensively cited review of the scientific literature. The author attempts to provide a mix of general features with chosen details while leaving out what he terms "specialist topics" like parasites, vascular and skeletal systems, physiology, and energetics. While understandable, it is unclear how some of those topics may have helped explain colony abandonments and other behaviors described in the text. The information presented is generally factual and accurate; although, with a treatise of this scope it is difficult to include all of the latest information that may substantiate or refute previously held views. For example, the notion that juvenile non-breeding American white pelicans (*Pelecanus erythrorhynchos*) return north from wintering areas to loaf or roost in colonies with breeding birds is contrary to current observations. However, omissions or disparities in the accounts are due more to a lack of published information on what are in many cases, economically insignificant and poorly studied species. The author did not appear enthralled with the concept of metapopulation biology being applied to these birds, at least not in the classical sense, while modified models have gained popularity to accurately describe population dynamics of some Pelecaniformes. The utility of the book is somewhat encumbered by the relatively brief index that hampers the ability to easily locate needed information. However, with few shortcomings, this volume will serve as a valuable and comprehensive reference for both the serious and amateur student of totipalmates.—JON J. (JEFF) DIMATTEO, North Dakota State University, Fargo, North Dakota; e-mail: jeff.dimatteo@ndsu.edu

GUÍA DE CAMPO A LAS AVES DE NORTEAMÉRICA [FIELD GUIDE TO THE BIRDS OF NORTH AMERICA]. By Ken Kaufman. Houghton Mifflin, New York, New York. 2005: 391 pp., 168 plates, and 631 maps. ISBN: 0-618-13219-8. $18.95 (soft back, waterproof).—Every time I show this guide to Spanish-speaking friends and colleagues they are pleasantly surprised and usually exclaim: "*está en Español!*"—it is in Spanish! This first ever Spanish-language field guide to the birds of North America published in spring 2005 targets an estimated 28 million U.S. Hispanics, but is also making a big impression among members of the conservation community—bird or otherwise—in Mexico.

The virtually identical Spanish version of Kaufman's acclaimed and updated *Field Guide to Birds of North America* is a comprehensive, pocket-size guide with a picture-illustrated table of contents that groups similar birds, even if they are not related. Each bird group or category is then referred to color-coded pages that present the birds' enhanced digital picture, distribution map, and description. This is all presented on two-page spreads making the guide user friendly.

Like its English-language counterpart, an innovative feature of this work is the use of digitally enhanced photographs to depict all birds described. Digital images combined with painting techniques highlight distinguishing field marks. This technology allows display of birds in a variety of ways: standing, flying, perching, feeding, etc. This deviation from the traditional bird drawing illustrations may be especially helpful for the beginner birdwatcher.

The introductory sections on getting started in birding covers, in a clear and concise manner, a suite of topics ranging from the difference between birding and bird watching, to keeping a life list, choosing binoculars, and the topography of a bird, to bird conservation and classification. The index of Spanish common names has check-off boxes in front of the name of the bird for the user to keep track of birds seen and to help build a life list. A short index of Spanish common names next to the index allows quick access to the page on which a bird or group of birds can be found. An additional short index of English common names would have proven particularly useful for bilingual birders just learning the Spanish common names.

Mexican ornithologist and bird conservationist Patricia Manzano Fischer translated the bird names. Although not a guide to the birds of Mexico, this book has the potential of becoming a well accepted reference to kick-off a much needed standardization of bird common names in that country. The particularly challenging translation of the descriptive terms of bird songs was accomplished by Mexican ornithologist Héctor Gómez de Silva by composing completely new Spanish birdsong descriptions.

The quality of the translation is, in my opinion, average to very good. Usually, one of the first reactions of the Spanish-speaking people to whom I have shown this book is: "*Guía de campo a las aves de Norteamérica . . . ? . . . it should be Guía de campo* **de** *las aves de Norteamérica!*" A minor translation glitch, mind you, but hard to miss in a book title. A side by side comparison of both language versions reveals numerous instances of straight, textual translation, making the Spanish version feel stiff and some times a bit disconcerting.

I join all the guide users with whom I have talked in praising this work as a great complement to other existing Spanish-language guides south of the border. The usefulness of its color-coded system, its compact size and portability, and the upgraded taxonomic changes all received high scores. Users also noted that several labels are missing on the bird topography and field marks illustration on page 12 ("tertials" and "rump"); that it would be best to include distribution or occurrence maps for all described birds including rare species; and that position of the letter "e" between bird size and bird wingspan in the raptors section can be easily confused as a typo.

This guide is sure to stand as a landmark in the busy field of guides to the birds of North America. The author is congratulated for his pioneering efforts in reaching out to the traditionally non-birding Hispanic community. This work, combined with additional outreach efforts by the birding community—this means: you!—in the growing Hispanic community should help move forward the author's belief that "we'll have more support for wildlife conservation if we have more people interested in nature". Get Kaufman's guide—in Spanish or English—take a Hispanic birding. Highly recommended.—JESÚS G. FRANCO, Texas Parks and Wildlife Department, McAllen, Texas: e-mail: Jesus.Franco@tpwd.state.tx.us

BIRDS OF THE WORLD: RECOMMENDED ENGLISH NAMES. By Frank Gill and Minturn Wright. Princeton University Press, Princeton, New Jersey. 2006: 272 pp. ISBN: 0691128278. $19.95 (paper).—This effort, sponsored by the International Ornithological Congress, provides standardized English names for all the known birds of the world, complementing the already published recommended names for French and Spanish (Devillers and Ouellet 1993, Bernis 1995). The book follows Howard and Moore's *Checklist of the Birds of the World,* Third edition (Dickinson 2003) with minor changes. The authors initially formed a committee of 30 people which developed the guidelines for the project, and formed six regional subcommittees where the majority of the work was done. Each subcommittee was assigned a list of names and identified the best English names to use. The subcommittees then commented on the work of the other subcommittees; the lists were then reviewed by the authors for compliance with the basic principles that had been adopted initially.

The committee initially agreed to use names of long standing, even if the names were inaccurate. Offensive names were eliminated, which removed some references to former countries, but not all. There was no option for having multiple accepted names in different regions; each species was to be assigned one and only one global English name. The name had to be unique for each species as well, which required modifiers for names that have been used for different species in different regions of the world. The full name of the species could not be a portion of another species name; each had to be unique again requiring modifiers. The list was to be of English names and other languages were not to be used except where the names were in common English usage, mostly from the native language of the region or from the scientific name.

While great thought went into the rules governing the selection of English names, even more thought went into the spelling and punctuation of the names, including the widespread use of hyphens in bird names. The committee agreed that bird names are capitalized, patronyms are possessive, and diacritical marks are not used. A compromise was reached for standards in spelling using British or American spelling rules: hyphens are minimized, compound words follow rules that address relationships between the words, and compound group names are hyphenated only to connect two names of birds or families of birds. This last rule has the greatest impact on the list from a North American perspective. Thus Black-crowned Night-heron (*Nycticorax nycticorax*) becomes Black-crowned Night Heron, and Common Ground-dove (*Columbina passerina*) becomes Common Ground Dove. Hyphens are retained where needed for clarity but otherwise are mostly eliminated from group names.

The list has a mix of European and American names for birds found in North America. Most are clearly from one side of the "pond" or the other, with notably few hybrids like the recommended Great Northern Loon for Common Loon (*Gavia immer*). Little Auk prevails for Dovekie (*Alle alle*), Pomarine Skua is used for Pomarine Jaeger (*Stercorcarius pomarinus*) (but the smaller Jaegers appropriately remain Jaegers), Sand Martin is used for Bank Swallow (*Riparia riparia*), Arctic Redpoll is used for Hoary Redpoll (*Carduelis hornemanni*), and Two-barred Crossbill for White-winged Crossbill (*Loxia leucoptera*). The modifier American is added for some species, including Cliff Swallow (*Petrochelidon pyrrhonota*) and White Ibis (*Eudocimus albus*). The new name Angel Tern is coined for White Tern (*Gygis alba*) due to conflicts with the name Fairy Tern (*Sterna nereis*), and the Rock Wren in New Zealand becomes the New Zealand Rockwren (*Xenicus gilviventris*), removing the potential conflict with the Rock Wren (*Salpinctes obsoletus*).

The book also lists regions where birds are found in an abbreviated way; of greater use is the CD that is included with an electronic table of the international English name, scientific name, breeding range (general region), more specific breeding range, and nonbreeding range where it is substantially different. This CD enhances the book greatly, making it more of a living document that can readily be used by other researchers and birders. The CD files are copyrighted, as is the rest of the material in the book, but the format enhances their utility. The book is remarkably free of typographical errors, reflecting great care in editing of the document. This book is recommended as a source for those in search of standardized English names for birds of the world, or a world list of birds.—MARY GUSTAFSON, Rio Grande Joint Venture Coordinator, Texas Parks and Wildlife Department, Mission, Texas; e-mail: mary.gustafson@tpwd.state.tx.us

BIRDS IN EUROPEAN CITIES. Edited by John G. Kelcey and Goetz Rheinwald. Ginster Verlag, St. Katharinen, Germany. 2005: 452 pp., 30 maps, 48 photographs, 30 tables, and 16 graphs. ISBN: 3-9806817-2-6. £29.50 (cloth).—This is an unusual book. At its heart are 16 chapters, each on a different European city. The selection is odd, with no obvious connection, and their randomness is emphasized by the presentation of chapters in alphabetical order of the city's English name. The cities are in 11 countries—Germany (3), Russia (2), Belgium, Spain, Portugal, Italy (2), Austria, Slovakia, Czech Republic, Bulgaria, and Poland (2)—but there is none from northern Europe (UK, Finland, Denmark, Sweden or Norway) or from France or The Netherlands.

As is implied by this comment, there is little uniformity of style across the 16 disparate chapters and, unfortunately, there is little attempt to analyze the important factors that affect the distribution and abundance of birds. This is a lost opportunity: with tighter editing or a comprehensive overview chapter, the editors could have provided some answers to the question implied by their comment "if a high quality environment is going to be created and maintained for people and 'nature' the design and management of cities will need to be directed by biologists." The cities chosen have grown under different political systems with differing degrees of centralized planning or relatively unconstrained development, offering potentially a good opportunity to deduce ecological conclusions and, thus, seek to influence future metropolitan developments.

The obvious species that opportunistically exploit newly created habitats or man-made nesting sites (such as White Stork [*Ciconia ciconia*], European Kestrel [*Falco tinnunculus*], Rock Pigeon [*Columba livia*], Swift [*Apus apus*], House Martin [*Delichon urbica*], House Sparrow [*Passer domesticus*], and Jackdaw [*Corvus monedula*]) in parks and open spaces in most cities are noted; the, at times, more extensive areas of woodland attract many others including woodpeckers and warblers. Indeed, almost every bird on the European list can be found in one of the cities, but inevitably the urban avifauna is dominated by a few, mostly generalist or anthropic species. One common factor—regrettable but perhaps inevitable—is that the warmer microclimate of cities has often favored establishment of alien species, especially parrots and geese.

A serious omission in this book is the lack of an index. This sadly diminishes its value as a reference work and, for instance, makes it almost impossible to contrast the avifauna of the different cities. There is a table of breeding species for all of the cities, but the only way of finding a species' status in other seasons is to read through every chapter! For instance, Bohemian Waxwings (*Bombycilla garrulus*) mainly frequent urban areas when they visit Britain in winter and I wondered about their winter distribution elsewhere; searching for this information proved to be an almost impossible task.

This volume could have been made more attractive and informative by well-chosen illustrations, but the few included—all in monochrome and printed with little contrast, giving a 'washed-out' appearance—do little to illuminate or enliven the book. I was interested to read the chapters about the cities in which I have lived or visited and I suspect that other readers will do likewise. But, I wonder who will want to go through the whole book.—DAVID NORMAN, Merseyside Ringing Group, England, and Carnegie Museum of Natural History, Powdermill Avian Research Center, Pennsylvania; e-mail: david.norman@physics.org

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Continued from outside back cover

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Volume 119, Number 2 CONTENTS June 2007

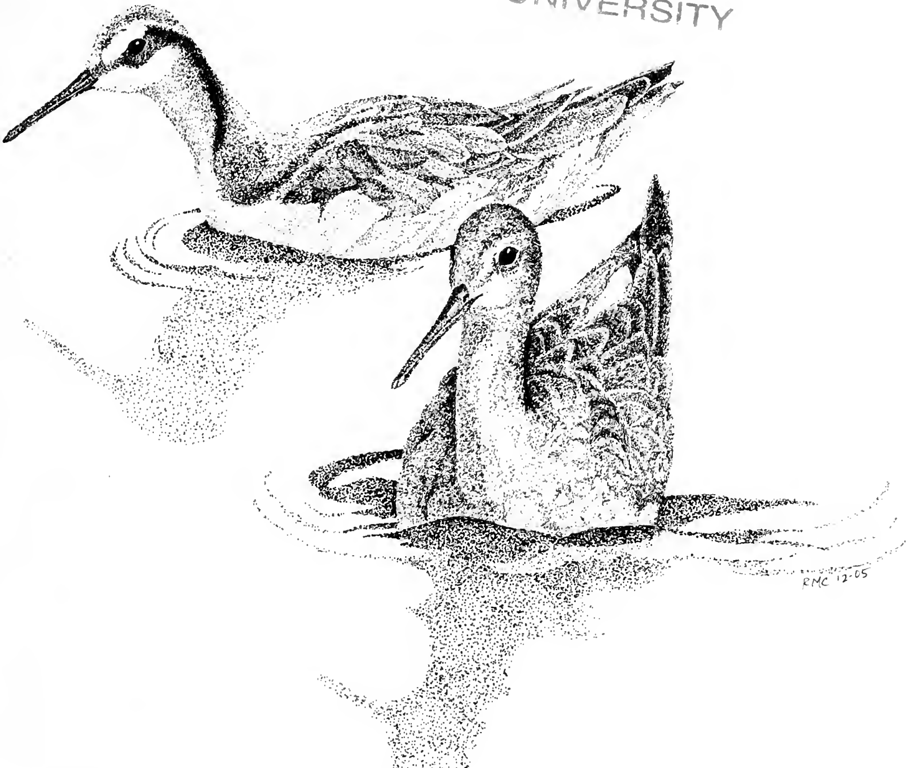
MAJOR ARTICLES

SHORT COMMUNICATIONS

Continued on inside back cover

The Wilson Journal *of Ornithology*

Volume 119, Number 3, September 2007



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COVER: Wilson's Phalaropes (*Phalaropus tricolor*). Illustration by Robin Corcoran.

FRONTISPIECE. ‘Elepaio (*Chasiempis sandwichensis*) from O‘ahu (upper left), Kaua‘i (upper right), and Hawai‘i (lower center). In addition to variation in plumage color among islands illustrated in these photographs, ‘Elepaio songs also differ among islands. VanderWerf (page 325) found that ‘Elepaio responded most strongly to songs from their own island and that response to foreign songs was asymmettical, providing insight into the history of colonization events among islands and indicating song may act as an isolating mechanism. Photographs by E. A. VanderWerf.

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BIOGEOGRAPHY OF ‘ELEPAIO: EVIDENCE FROM INTER-ISLAND SONG PLAYBACKS

ERIC A. VANDERWERF[1]

ABSTRACT.—I used inter-island song playbacks and information on geology, ecology, and behavior to investigate biogeography and species limits in the ‘Elepaio (*Chasiempis sandwichensis*), a monarch flycatcher (Monarchidae) endemic to the Hawaiian Islands. ‘Elepaio occur on Kaua‘i, O‘ahu, and Hawai‘i, but are absent on the four islands of the Maui Nui group in the center of the Hawaiian Archipelago. It is unlikely that ‘Elepaio became extinct on Maui Nui or were excluded by the presence of competing species. ‘Elepaio are absent in the fossil record on all four islands of Maui Nui, but occur in the fossil record on all three islands they currently inhabit. They have adapted to a variety of forested habitats and are more resistant to alien diseases than other bird species that have persisted on Maui Nui. ‘Elepaio on each island responded most strongly to songs from their own island. Response to foreign songs was asymmetrical. Hawai‘i ‘Elepaio responded to songs from Kaua‘i, suggesting that ‘Elepaio on Kaua‘i and Hawai‘i share a more recent common ancestry. The sequence of colonization events that led to the current distribution was most likely: (1) Kaua‘i to O‘ahu and (2) Kaua‘i to Hawai‘i. Geologic and genetic evidence indicate the ‘Elepaio lineage arrived in the Hawaiian Islands ~1.5–1.9 million years ago. ‘Elepaio probably were blown from Kaua‘i to Hawai‘i during storms, skipping several of the stepping-stones in the Hawaiian chain. The low level of foreign song recognition indicates song could inhibit interbreeding and might serve as an isolating mechanism. *Received 13 February 2006. Accepted 8 November 2006.*

The ‘Elepaio (*Chasiempis sandwichensis*) is a monarch flycatcher (Monarchidae) endemic to the Hawaiian Islands. ‘Elepaio occur on the islands of Kaua‘i, O‘ahu, and Hawai‘i, but are absent on the four islands of the Maui Nui group (Maui, Moloka‘i, Lana‘i, and Kaho‘olawe) in the center of the Hawaiian Archipelago (Pratt et al. 1987, VanderWerf 1998). ‘Elepaio have been classified into three or more taxa based primarily on plumage differences, each found on a single island. Each island taxon was originally described as a separate species: *C. sandwichensis* Gmelin 1789 on Hawai‘i; *C. ibidis* Stejneger 1887 (formerly *C. gayi* Wilson 1891) on O‘ahu; and *C. sclateri* Ridgway 1882 on Kaua‘i (Pratt 1980, Olson 1989, VanderWerf 1998). These taxa were later reclassified as subspecies by Bryan and Greenway (1944) without any explanation or justification, and this taxonomy has been followed since. Some authorities continue to treat them as species (Olson and James 1982, Conant et al. 1998), and the American Ornithologists’ Union is considering a taxonomic

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revision of ‘Elepaio in which the forms on different islands would again be separated as species (AOU 2000). Two additional subspecies, *C. s. ridgwayi* and *C. s. bryani*, are recognized on Hawai‘i by some authorities, based on variation in plumage color on the head, back, and breast (Henshaw 1902, Pratt 1979, Pratt 1980).

The Hawaiian Islands are volcanic in origin and were formed sequentially as the Pacific plate of the earth’s crust moved northwest over a “hot spot” where magma from the mantle reaches the surface (Walker 1990, Carson and Clague 1995). The most common biogeographic pattern in the Hawaiian Islands is that of a stepping stone or conveyor belt where organisms sequentially colonized each new island from west to east (Freed et al. 1987, Wagner and Funk 1995, Fleischer et al. 1998, Fleischer and MacIntosh 2001). The absence of ‘Elepaio on Maui, Moloka‘i, Lana‘i, and Kaho‘olawe is peculiar given the ordered geologic history of the Hawaiian Islands. There are two possible explanations for this absence: (1) ‘Elepaio have become extinct on these islands or (2) ‘Elepaio never occurred on these islands, or at least failed to become established on them. These four islands formed a single island called Maui Nui (literally “big Maui”) during prehistoric periods of lower sea level (Carson and Clague 1995, Price and Elliott-Fisk 2004), and the absence of ‘Elepaio on all four islands could be related.

Vocalizations can provide important information in studies of avian biogeography and systematics (Payne 1986, Isler et al. 1998). Song is involved in species recognition in many birds (Catchpole and Slater 1995), can change rapidly through cultural evolution (Payne 1986), and may have an important role in speciation (Martens 1996). The importance of geographic variation in song can vary but, in some cases, it provides a clue to underlying patterns of cryptic morphological variation and reproductive isolation (Groth 1993, Balakrishnan and Sorenson 2006). Playbacks of recorded songs can be a useful method of demonstrating whether song may act as an isolating mechanism (Grant and Grant 2002, Balakrishnan and Sorenson 2006). The objectives of this study were to investigate biogeography and species limits in ‘Elepaio using inter-island song playbacks, and to assess the possibility that ‘Elepaio have become extinct on Maui Nui using information on geology, ecology, and behavior.

METHODS

The primary song of ‘Elepaio, given almost exclusively by males, is used in territory defense and mate attraction (VanderWerf 1998). Female ‘Elepaio often respond to this song with a distinctive two-note call. The primary song differs somewhat among islands, having the fewest phrases and least frequency modulation on Kaua‘i and the most on Hawai‘i (Fig. 1; VanderWerf 1998). There is some song variation within islands, but the extent of variation within islands is much less than among islands (Fig. 1; E. A. VanderWerf, unpubl. data). The Hawaiian name ‘Elepaio is derived phonetically from this song.

I conducted three song playback experiments with ‘Elepaio: one on O‘ahu in Kuli‘ou‘ou and Pia valleys on 29 February 1996, one on Kaua‘i along the Mōhihi-Wai‘alae Trail in the Alaka‘i Wilderness Preserve on 5 April 1996, and one on Hawai‘i at Hakalau Forest National Wildlife Refuge on 21 April 1996. ‘Elepaio remain paired and defend territories year-round, but territorial aggression peaks just prior to and during nest construction, declines rapidly once incubation begins, and remains low during the nonbreeding season (VanderWerf 1998, VanderWerf and Freed 2003). Playback experiments were timed to coincide with the usual peak in nest construction on each island to ensure the strongest possible response (VanderWerf 1998).

I used a Marantz PMD222 cassette recorder and a Telinga microphone and parabolic reflector to record primary songs and calls of adult males at each site. I made 1-min loop cassettes from these recordings that consisted of songs and calls from three different adult males at each site to reduce pseudoreplication (Catchpole 1989, Kroodsma 1989). Male ‘Elepaio often intersperse calls between series of songs, and calls were included with songs on the cassettes in an attempt to make the recordings sound more realistic. Sound spectrograms of male ‘Elepaio songs were prepared using Raven 1.2 (Cornell Laboratory of Ornithology 2004).

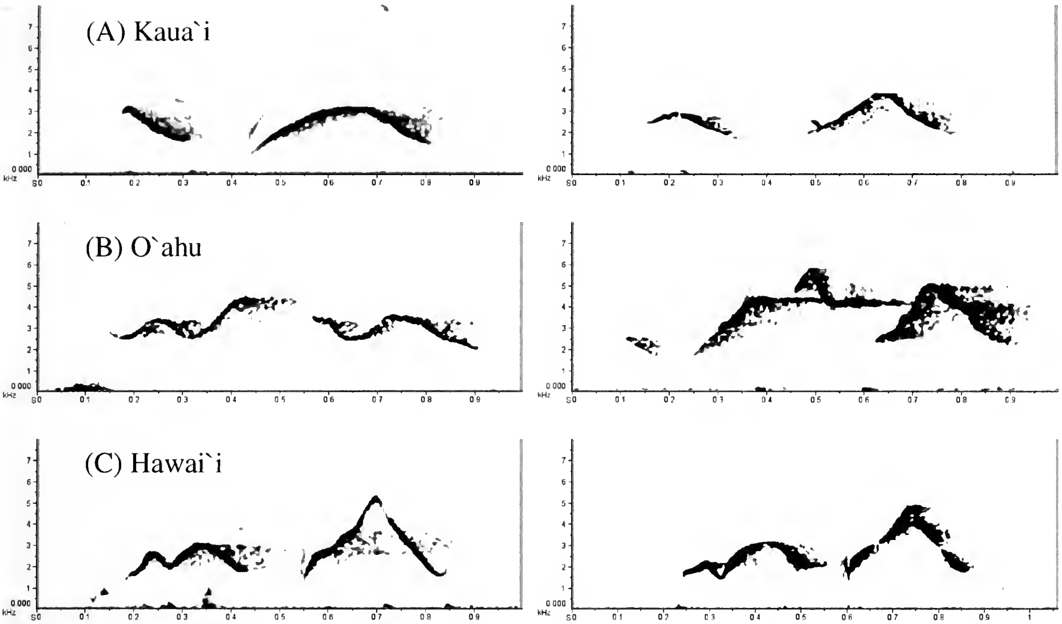

FIG. 1. Sound spectrograms of songs from male ‘Elepaio on (A) Kaua‘i, (B) O‘ahu, and (C) Hawai‘i. Single songs from two different males on each island.

Nine male ‘Elepaio were used as experimental subjects at each site. It would have been useful to examine the response by female ‘Elepaio to assess the extent of intersexual selection, but during playback tests females generally followed the male and their response was not independent. None of the recordings used in the playbacks was from any of the subjects or their neighbors. Recordings from each island were played to each subject for 3 min, with a 3-min rest period between playbacks, so the total duration of a trial with each subject was 15 min (island one, rest; island two, rest; island three). The order in which recordings were played was systematically varied among subjects so that recordings from a given location were played first, second, and third an equal number of times (three). The playback length was deliberately short to reduce potential habituation (a decline in response strength in later trials).

Recordings were broadcast through a speaker placed on the ground in the approximate geographic center of each subject’s territory because aggressiveness of response often declines toward territory margins (Melemis and Falls 1982). Recordings were played from a Sony TCM cassette player connected to the speaker by a 10 m cable. Observations were made from a position next to the cassette player.

Response by each subject to each 3-min playback was measured with three variables: vocal response, physical response, and latency (time to first vocal or physical response). Each variable was scored on a scale from 0 to 4 (Table 1). Categories of physical response were chosen so they represented progressively more aggressive behaviors. Approach distance was measured from the speaker. A “song display” was a distinctive behavior in which songs were delivered while the feathers on the throat and crown were erected, the tail was held at 90° and fanned to display the white tips, and the wings were drooped to expose the white wing bars and rump (VanderWerf 1998). A “swoop” was when a bird dove toward the speaker. Categories of latency and vocal response were chosen so the distribution of observations was as close as possible to normal.

An overall response score ranging from 0 to 12 was derived by summing the scores of the three variables. Variation in response by birds on each island was examined with a General Linear Model using overall response

TABLE 1. Variables used to measure strength of response by male ‘Elepaio during song playbacks. Latency was measured as the time to first response (song or approach). A single overall measure of response strength ranging from 0 to 12 was derived for use in analyses by summing the scores from all three variables.

Latency (sec)	Number of songs	Physical approach	Score
No response	0	None	0
>60	1–5	Distant approach (>10 m)	1
20–60	6–10	Close approach (<10 m)	2
10–19	11–20	Song display	3
<10	>20	Swoop	4

score as the dependent variable and song type (Kaua‘i, O‘ahu, or Hawai‘i), song order (first, second, or third), and individual bird as independent variables. Pair-wise tests were conducted between groups using Tukey’s correction for multiple comparisons if there was significant overall variation in response.

‘Elepaio are naturally curious and can be attracted by a variety of sounds, including human voices and “pishing” (VanderWerf 1998). Thus, a low level of response can be expected to any persistent loud sound in the territory. Weak responses to playbacks were interpreted with caution and greater emphasis was placed on the relative response to different treatments. I considered using songs of another monarch flycatcher, a different bird species, or another sound as a control, but elected not to do so because of the increased potential for habituation that might have resulted from an additional trial with each subject.

RESULTS

‘Elepaio on each island responded most strongly to songs from their own island (Fig. 2). Responses to foreign songs were weaker and did not differ in most cases (Fig. 2). For example, ‘Elepaio on Kaua‘i responded more strongly to songs from Kaua‘i than to songs from O‘ahu or Hawai‘i, and response to songs from O‘ahu and Hawai‘i did not differ (Fig. 2A; $F_{2,14} = 15.33$, $P < 0.001$). Similarly, ‘Elepaio on O‘ahu responded more strongly to songs from O‘ahu than to songs from Kaua‘i or Hawai‘i, and response to songs from Kaua‘i and Hawai‘i did not differ (Fig. 2B; $F_{2,14} = 12.30$, $P = 0.002$). However, ‘Elepaio on Hawai‘i responded more strongly to songs from Hawai‘i and Kaua‘i than to songs from O‘ahu (Fig. 2C; $F_{2,14} = 4.92$, $P = 0.02$).

The nature of the responses to foreign songs also is instructive. On O‘ahu, seven of nine birds did not sing in response to either foreign song and responded with only a distant (>10 m) approach. On Kaua‘i, four of nine birds did not sing in response to either foreign song, and six and five birds responded with only a distant approach to songs from O‘ahu and Hawai‘i, respectively. On Hawai‘i, all birds except one sang in response to all songs, although most birds sang more often in response to songs from Hawai‘i.

There was no evidence that habituation occurred in any of the three experiments. Response strength was not affected by the order in which songs were played ($F_{2,14}$ = 0.42, 0.73, and 0.76, P = 0.66, 0.51, and 0.48 on Kaua‘i, O‘ahu, and Hawai‘i, respectively). There was some tendency for certain birds to respond more strongly, but the overall levels of individual variation were not significant ($F_{8,14}$ = 1.59, 2.16, and 1.73, P = 0.22, 0.14, and 0.18 on Kaua‘i, O‘ahu, and Hawai‘i, respectively).

DISCUSSION

Are ‘Elepaio Reproductively Isolated Among Islands?

Mitochondrial DNA evidence indicates there is little or no gene flow among islands and the extent of differentiation in ‘Elepaio among islands is consistent with species level differences (Burgess 2005). In addition to the obvious physical barrier posed by the Pacific Ocean, low levels of foreign song recognition among islands could serve as an additional premating isolation mechanism. There is no information on song learning in ‘Elepaio, but it is likely they learn songs from adult tutors early in their developmental period like virtually all oscine passerines (Catchpole and

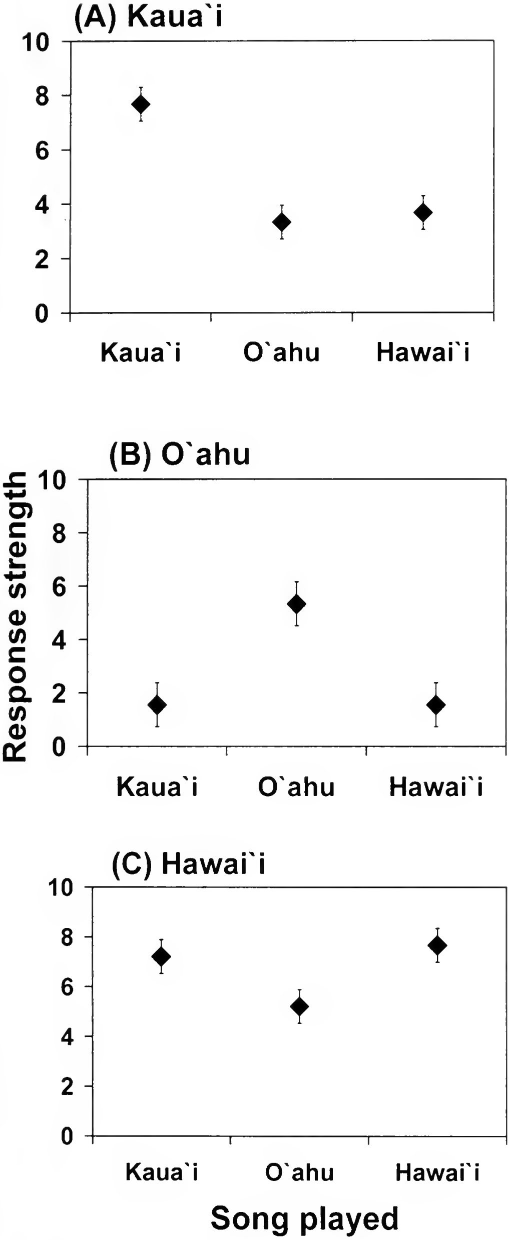

FIG. 2. Responses of male ‘Elepaio on each island to songs from each island (mean ± SE). Response strength includes number of songs, physical approach, and latency of response.

Slater 1995). Recent evidence indicates birds retain a long-lasting memory of the tutor's song that largely shapes their own song (Phan et al. 2006). Young ‘Elepaio remain with their parents on the natal territory for up to 9 months (VanderWerf 2004). They learn complex foraging behaviors during this time (VanderWerf 1994) and begin to sing just prior to the onset of the next breeding season. Island-specific song dialects may have arisen through founder events and geographic isolation (Matessi et al. 2000, Wright and Dorin 2001); these local dialects may be reinforced through foreign song avoidance. ‘Elepaio that emigrated to another island thus might not be recognized as potential mates based on their songs, or at least might not be preferred, leading to reproductive isolation (Balakrishnan and Sorenson 2006).

Colonization History and Timing

The stronger response by Hawai‘i ‘Elepaio to songs from Kaua‘i than to songs from O‘ahu suggests ‘Elepaio on Kaua‘i and Hawai‘i share a more recent common ancestry and the O‘ahu ‘Elepaio is most divergent. The sequence of colonization events that led to the current distribution was most likely: (1) Kaua‘i to O‘ahu and (2) Kaua‘i to Hawai‘i (Fig. 3). However, the direction of colonization between Kaua‘i and O‘ahu cannot be inferred with certainty based on song playbacks alone.

The pattern of response between Kaua‘i and Hawai‘i was asymmetrical; Hawai‘i ‘Elepaio responded to songs from Kaua‘i, but Kaua‘i ‘Elepaio did not respond to songs from Hawai‘i. This suggests ‘Elepaio respond more strongly to songs of their ancestors than to songs of their descendents. Such asymmetrical behavioral isolation, in which ancestral populations discriminate against courtship displays of derived populations but derived populations accept displays of their ancestors, was first described in Hawaiian *Drosophila* (Kaneshiro 1976, Kaneshiro and Giddings 1987) and has become known as the Kaneshiro hypothesis. The mechanism originally proposed for the behavioral asymmetry was loss of certain elements of the courtship display during founder events, but Ohta (1978) proposed that founder events also could involve selection for decreased female discrimination. It is not clear why only Hawai‘i ‘Elepaio recognized ancestral songs, since either Kaua‘i or O‘ahu must have been ancestral to the other. Ancestral song recognition may decrease over time due to gradual accumulation of changes in

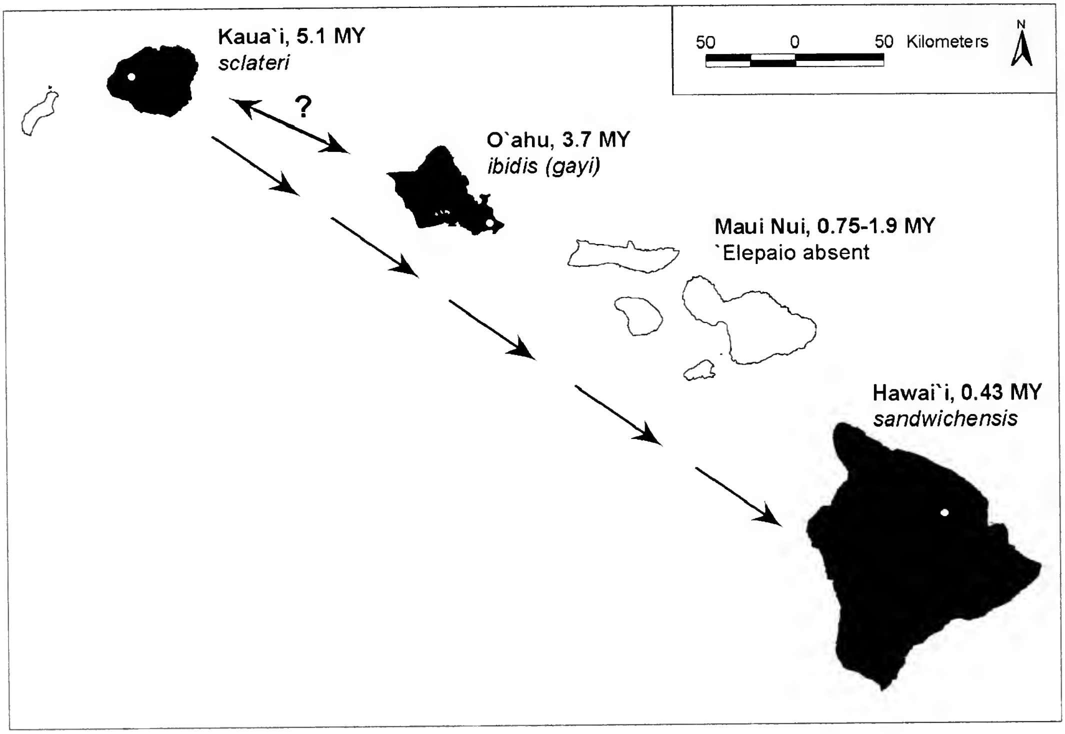

FIG. 3. ‘Elepaio occur on the Hawaiian islands of Kaua‘i, O‘ahu, and Hawai‘i, but are absent from Maui Nui (Maui, Moloka‘i, Lana‘i, and Kaho‘olawe), even in the fossil record. Island ages in millions of years (MY) from Carson and Clague (1995). Evidence from song playbacks suggests ‘Elepaio on O‘ahu diverged first, but the direction of colonization is not certain, and that Hawai‘i was colonized directly from Kaua‘i. Study sites are marked with a dot.

song or to reversal in selection for decreased female discrimination with increasing population size. The Kaneshiro hypothesis has been demonstrated in other groups of Hawaiian *Drosophila* (Koepfer and Fenster 1991) and in Hawaiian crickets of the genus *Laupala* (Shaw and Lugo 2001). If further analysis of genetic data corroborates the colonization sequence indicated by song playback experiments, this would represent the first demonstration of the Kaneshiro hypothesis in a bird. Male song represents only one aspect of courtship behavior in ‘Elepaio, which also involves courtship feeding and mock chases (VanderWerf 1998); comparison of these behaviors among islands could provide additional evidence.

A combination of genetic and geological evidence indicates ancestral ‘Elepaio arrived in the Hawaiian Islands 1.5–1.9 million years (myr) ago. Mitochondrial DNA analysis indicates the ‘Elepaio lineage is at least 1.5 myr old (Filardi and Moyle 2005). O‘ahu and western Moloka‘i were connected about 1.9–2.2 myr ago, forming the larger island of O‘ahu Nui, but the saddle connecting the volcanoes on these islands was submerged due to island subsidence and rising sea level (Price and Elliott-Fisk 2004). If ‘Elepaio existed on O‘ahu when it was connected to Moloka‘i, they presumably would have occupied both islands. This apparently was not the case, indicating the ‘Elepaio lineage is less than 1.9 myr old. Given the age of each island (Fig. 3), either Kaua‘i or O‘ahu could have been the first island colonized, but Hawai‘i could not.

‘Elepaio and other Pacific island monarchs are non-migratory and quite sedentary (Sanders et al. 1995, VanderWerf 2004), and it is unlikely that ‘Elepaio deliberately flew between islands. Natal dispersal distances of ‘Elepaio are usually less than a kilometer (VanderWerf 1998) and breeding dispersal distances of adults are usually only a few hundred meters (VanderWerf 2004), although some longer distance dispersal may occur rarely (Burgess 2005). It is more likely that ‘Elepaio were carried to new islands by strong winds during rare storm events and made landfall on the first island in their path. Hawai‘i can be reached from Kaua‘i without passing directly over O‘ahu or Maui Nui because Hawai‘i is slightly south of the line formed by the other islands (Fig. 3). If Hawai‘i had been colonized from O‘ahu, birds would have passed directly over or very close to Maui Nui, making their absence more difficult to explain. Similar disjunct distributions, in which sister taxa occur on non-neighboring islands, are known in several other Hawaiian groups, including picture-winged flies (Drosophilidae), yellow-faced bees (Colletidae), and numerous plants (K. Y. Kaneshiro, K. R. Wood, and Karl Magnacca, pers. comm.). Most of these cases involve Kaua‘i and one or more younger islands.

Have ‘Elepaio Become Extinct on Maui Nui?

Several lines of evidence indicate ‘Elepaio have not become extinct on Maui Nui. The most compelling evidence against extinction is that ‘Elepaio are absent in the fossil record on all four islands in Maui Nui, but occur in the fossil record on all three islands they currently inhabit (Olson and James 1982, James and Olson 1991, Burney et al. 2001). The adaptability of ‘Elepaio also suggests it is unlikely ‘Elepaio became extinct on Maui Nui or were excluded by the presence of competing species. ‘Elepaio are flexible in habitat selection (VanderWerf 1993), use a wide range of foraging behaviors, forage at all heights and on many substrates (VanderWerf 1994), prey on a variety of invertebrates (VanderWerf 1998), and have adapted to a wide range of forest types including lowland wet forest, montane cloud forest, dry subalpine shrubland, small pockets of forest isolated by recent lava flows (kipukas), and disturbed forest dominated by alien plant species (Conant 1977, van Riper 1995, VanderWerf 1998, VanderWerf and Smith 2002, VanderWerf 2004). ‘Elepaio also have greater immunity than many Hawaiian forest birds to alien diseases that have decimated the endemic avifauna (van Riper et al. 1986, Atkinson et al. 1995, VanderWerf 2001). Finally, Maui is a large island that has retained extensive areas of native forest and still supports several Hawaiian honeycreepers (Drepanidinae) that are much more sensitive to disturbance and disease than ‘Elepaio (Pratt et al. 2001, Groombridge et al. 2004). It is possible that too few ‘Elepaio reached Maui Nui to establish a breeding population, but it is unlikely that ‘Elepaio have become extinct on Maui Nui. If extinction is ruled out, the biogeography of ‘Elepaio does not follow the typical stepping stone pattern found in other Hawaiian bird taxa (Freed et al. 1987, Fleischer et al. 1998).

This study demonstrates there is lack of recognition of foreign songs among male ‘Elepaio indicating birds from other islands are not recognized as potential competitors for mates (Balakrishnan and Sorenson 2006). Demonstration of foreign song avoidance by females would provide important additional evidence of reproductive isolation, although this may prove difficult in a field setting. Further investigation of molecular genetic divergence among and within ‘Elepaio populations on each island would aid examination of their phylogeography and taxonomy. Finally, quantitative examination of vocal characters would help corroborate the results of this study.

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FLIGHT CALLS OF WOOD-WARBLERS ARE NOT EXCLUSIVELY ASSOCIATED WITH MIGRATORY BEHAVIORS

ANDREW FARNSWORTH[1]

ABSTRACT.—Wood-warblers (Parulidae) have species-specific flight calls given day and night in migration. These vocalizations are believed to maintain flocks and to stimulate migratory activity during migration. However, anecdotal evidence suggests that warblers also give flight calls during non-migratory periods. I examined use of flight calls during the nesting, fledgling, and wintering periods in 23 species of warblers to clarify the seasonal pattern of occurrence for this type of vocalization. Flight calls recorded during migratory and non-migratory periods were similar. The Nashville Warbler (*Vermivora ruficapilla*) was the only species that gave flight calls during the nesting period and it did so rarely. Half of the species surveyed during fledgling periods and nearly half (47.8%) of the species surveyed during wintering periods gave flight calls. Calls per minute rates during the nesting period were an order of magnitude lower than in the fledgling and wintering periods. Flight calls are most common during migration but this vocalization in warblers is not limited to migratory periods. Flight calls may have functions additional to those during migration. *Received 25 May 2006. Accepted 26 December 2006.*

Flight calls are species-specific notes that are usually less than 300 milliseconds in duration and generally in the 1–11 kHz range. They can be pure tones or modulated and occasionally calls represent several syllables. These vocalizations are generally narrow in bandwidth and high in frequency, and are distinctly different from broad bandwidth and lower frequency alarm calls or contact notes. Flight calls are significantly higher in pitch, narrower in bandwidth, and shorter in duration than notes that compose bird song (Farnsworth and Lovette 2005).

Many species of birds use flight calls during migratory periods (Evans and O'Brien 2002, Farnsworth 2005). However, flight calls also occur in certain species' repertoires outside of migration (e.g., *Catharus*; Evans 1994, Evans and O'Brien 2002). Thus, comprehensive evaluation of the functions of flight calls must address their prevalence and use in both migratory and non-migratory periods. The objective of this paper is to present the first data available on seasonal patterns of flight-calling in 23 species of wood-warblers (Parulidae, hereafter warblers) in non-migratory breeding and over-wintering periods.

METHODS

I observed 23 species of warblers during three different non-migratory periods between December 2003 and January 2006. The pre-fledging period (hereafter the nesting period) was from 1 June to 14 July 2003 at which time no young birds were present outside the nest. The post-fledging period (hereafter the fledgling period) was from 1 July to 1 August 2004 when young had left the nest but still traveled in the company of adults. The non-breeding over-wintering period (hereafter the wintering period) was from 27 December to 27 February between 2003 and 2006 at which time birds traveled in flocks or individually, or birds established territories (Table 1). I observed individuals for 10-min periods in daylight hours between pre-dawn and post-sunset civil twilights, noting presence and number of flight calls. I broadly define the timing of these observation periods in local Standard time as early, dawn civil twilight to 0900 hrs; midday, 0900 to 1500 hrs; and late, 1500 hrs to dusk civil twilight. I selected the timing of these observation periods at random prior to any observations. I recorded flight calls using a Sennheiser MKH 70 microphone. Analog and digital data were recorded with a Sony TCM-5000 to cassette and a Nagra Ares BB+ to flash memory, respectively. All flight calls were either recorded or digitized at 16-bit, 22050 Hz sampling rates as uncompressed .WAV files. I used a spectrographic cross correlation and principal coordinate ordination technique (SPCC; after Clark et al. 1987 and Cortopassi and Bradbury 2000, 2006; following Farnsworth 2007; unpublished software

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from K. A. Cortopassi) to compare flight-call recordings from non-migratory periods with previously published recordings from migratory periods (Evans and O'Brien 2002). I plotted the first and second principal coordinates (PCOs), representing approximately 89% of the original variation among calls, to represent flight-call similarity.

RESULTS

Flight calls recorded outside migratory periods were similar to those of known individuals recorded during migratory periods by visual inspection (Fig. 1) and, more importantly, by SPCC (Fig. 2, data shown for American Redstart [*Setophaga ruticilla*] only). The Nashville Warbler (*Vermivora ruficapilla*) was the only one of the 16 species observed during the nesting period (140 observation periods during 23 hrs and 20 min) that gave flight calls and these three flight calls occurred during two periods (Table 2). Five of the 10 species observed during the fledgling period (61 observation periods during 10 hrs and 10 min) had 42 flight calls recorded during 13 periods (Table 2). Eleven of 23 species (47.8%) observed during the wintering period (248 observation periods during 41 hrs and 20 min) had 127 flight calls recorded during 43 periods (Table 2). Nashville (48 of 127 calls) and Cape May (*Dendroica tigrina*) (43 of 127 calls) warblers represented 37.8 and 33.9% of the calls, respectively (Table 2). The nesting period had an order of magnitude of lower calls per minute rate than fledgling and wintering periods when call counts were standardized by observation periods (Table 2).

I recorded more calls and a higher percentage of observation periods with calls during the early period of the day within each seasonal period than during the two later periods of the day (Fig. 3). The highest percentage of observation periods with calls occurred in the early fledgling period (Fig. 3). Percentage of intervals with calls in midday and late periods did not differ for fledgling and wintering periods, nor did fledgling and wintering periods differ in percentage of periods with calls (Fig. 3). However, I recorded many more calls in midday and late periods during the wintering interval.

TABLE 1. Observations of flight-calling behavior for 23 species of warblers.

Year	Location	Status	Dates	Days	Observation periods				Species recorded	Species giving calls
					Early[b]	Midday[c]	Late[d]	Totals		
2003	Adirondacks and Finger Lakes, NY, USA	Nesting	1 Jun–14 Jul	27	58	39	43	140	16	1
2004	Adirondacks and Finger Lakes, NY, USA	Fledgling	1 Jul–1 Aug	10	23	25	13	61	10	5
2004	Eastern Cuba[a]	Wintering	31 Jan–27 Feb	22	81	70	38	189	18	9
2003–04	Cuernavaca, Morelos, Mexico	Wintering	27 Dec–2 Jan	7	8	5	5	18	9	3
2004–05	Cuernavaca, Morelos, Mexico	Wintering	27 Dec–3 Jan	8	4	3	10	17	6	2
2005–06	Cuernavaca, Morelos; Careyes, Jalsico, Mexico	Wintering	27 Dec–7 Jan	12	11	6	7	24	6	2

[a] Cayo Guam, Bahia de Taco, Nuevo Mundo, Bario Nuevo, Uvero, Santiago, Gran Piedra.
[b] Dawn civil twilight to 0900 hrs, local Standard time.
[c] 0900 to 1500 hrs, local Standard time.
[d] 1500 hrs to dusk civil twilight, local Standard time.

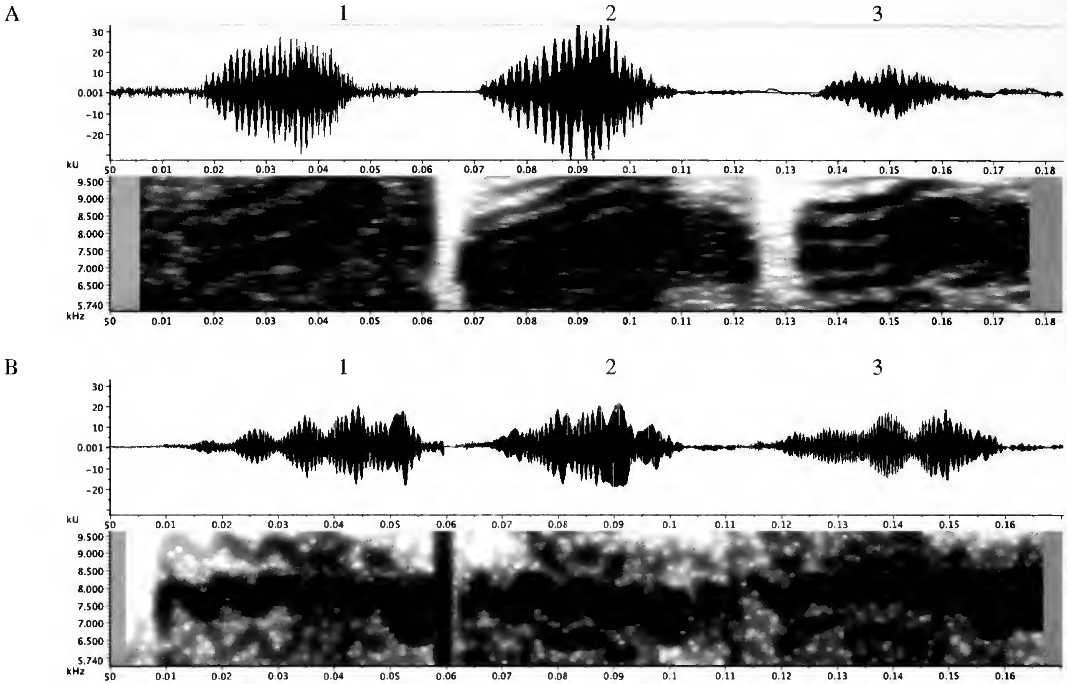

FIG. 1. Flight calls of (A) Nashville Warbler recorded during three different seasonal periods: (1) migration (Sep 2004, Ithaca, NY, USA), (2) nesting (Jun 2003, Adirondacks SP, NY, USA), and (3) wintering (Dec 2004, Morelos, Mexico); and (B) Cape May Warbler recorded during two different seasonal periods: (1) migration (May 2005, New York, NY, USA) and (2) wintering (Feb 2004, Humboldt National Park, Cuba). Flight calls are shown as waveform (upper ordinate axis) and spectrogram (lower ordinate axis) representations.

DISCUSSION

The published literature on flight-calling behavior focuses on its occurrence during migratory periods, especially at night (Ball 1952, Evans and O'Brien 2002, Farnsworth 2005). Individual warblers can produce more than 200 calls in a 10-min period during migration (captive Tennessee Warbler [*Vermivora peregrina*] in fall; A. Farnsworth and M. Lanzone, unpubl. data). However, flight calls are not restricted to these periods. Flight calls outside of migration are less common than during migration, but almost half of the total warbler species surveyed across all periods in this study gave diurnal flight calls at some point during non-migratory periods. Nearly half of the species surveyed in winter and in post-fledging periods gave flight calls. Only one species, the Nashville Warbler, gave flight calls during the nesting season and these were rare.

Temporal patterns of calling vary extensively at night (e.g., Farnsworth et al. 2004), and variation may also exist in diurnal patterns of vocalization. I counted more calls and found a higher percentage of observation periods with calls before 0900 hrs local standard time for all seasonal periods. However, I recorded numerous calls during observation periods later in the day in the fledgling and wintering periods. Flight calls likely occur during all times of the day during most of the year with the exception of the nesting period. However, finer temporal resolution would clarify the extent of this variation and more information, particularly for multiple species from multiple study sites for multiple years, is necessary to quantify the variation in calling that may occur among seasons.

Non-migration related flight-calling behavior is substantially more prevalent during winter and post-fledging periods (17.4 and 21.3% of periods, respectively) than during the pre-hatching period of the nesting season (1.4% of periods). This pattern is particularly striking when calls are standardized by observation time (Table 2). Flight calls are a regular,

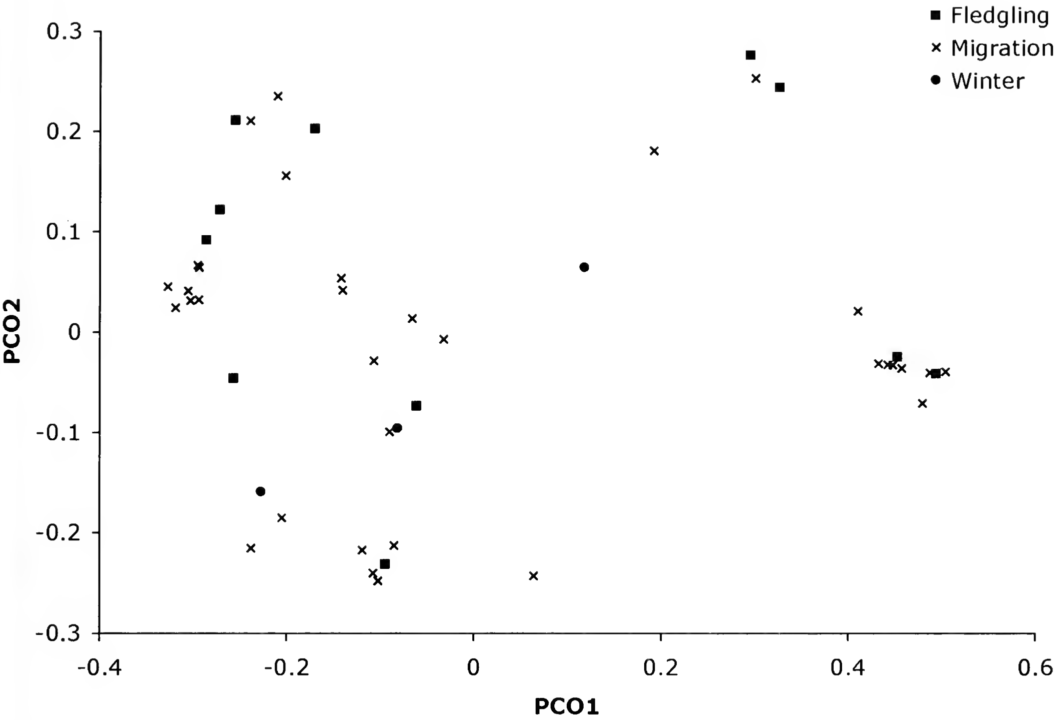

FIG. 2. Scatter plot of principal coordinate 2 (PCO2) against principal coordinate 1 (PCO1) showing the similarity among American Redstart flight calls recorded during fledgling, wintering, and migratory periods.

albeit small, part of warbler vocal repertoires during much of the year. The occurrence of flight calls at all times of the year other than the nesting season, when birds are on territory and incubating, suggest the possibility of a general function for these calls in addition to more specific functions they may have during migration.

Facilitating group cohesion appears to be a likely function of these vocalizations. Flight calls are short, high frequency, narrow bandwidth vocalizations, ideal for short-distance communication. These calls may also fall outside the range of hearing of some predators (Dooling 1982, Okanoya and Dooling 1987, Langemann et al. 1998, Gill and Sealy 2003, Farnsworth and Lovette 2005; but see Shalter and Schleidt 1977, Klump and Shalter 1984). Perhaps more likely, however, is that flight calls have a grouping role among recently fledged birds foraging with adults in family groups. The short, high frequency signals may function to reduce fear or indicate intentions that are not aggressive or territorial, functions that are characteristic of vocal behaviors of family foraging groups.

Warblers that give flight calls in winter may also use them in much the same way as recently fledged birds traveling with adults, to promote integration with non-threatening intentions into mixed species flocks. For example, Nashville Warblers forage in mixed species flocks in winter in western Mexico (Hutto 1980, 1994; Howell and Webb 1995; Williams 1996) and this species gives flight calls with some regularity (Table 2). Similarly, Cape May Warblers in Cuba gave flight calls more than any other local species observed and nearly as often as the Nashville Warbler (Table 2; A. Farnsworth, unpubl. data), particularly in context of mixed species flocks led by resident Oriente Warblers (*Teretistris fornsi*). Both Nashville and Cape May warblers also engage in local facultative movements often involving groups (Baltz and Latta 1998). Similarly, Yellow-rumped Warblers (*Dendroica coronata*), which flock extensively on wintering areas, engage in facultative nocturnal

TABLE 2. Flight calls for 23 species of warblers. Each period represents a 10-min observation.

	Nesting[a]				Fledgling[b]				Winter[c,d,e,f]				
Species	Calling periods	Total periods	Calls	Calls/ min	Calling periods	Total periods	Calls	Calls/ min	Calling periods	Total periods	Calls	Calls/ min	All Total periods
American Redstart (*Setophaga ruticilla*)	0	11	0	0	3	12	12	0.1	2	14	3	0.02	37
Black-and-white Warbler[c,e,f] (*Mniotilta varia*)	0	8	0	0	0	4	0	0	4	14	6	0.04	26
Black-throated Blue Warbler (*Dendroica caerulescens*)	0	9	0	0	2	7	4	0.06	2	37	4	0.01	53
Black-throated Gray Warbler[e,f] (*D. nigriscens*)									0	5	0	0	5
Black-throated Green Warbler[c,e,f] (*D. virens*)	0	10	0	0	2	6	12	0.2	0	9	0	0	25
Cape May Warbler (*D. tigrina*)									14	34	43	0.13	34
Chestnut-sided Warbler (*D. pennsylvanica*)	0	5	0	0	4	8	11	0.14					13
Common Yellowthroat (*Geothylpis trichas*)	0	11	0	0	0	6	0	0	2	9	4	0.04	26
Hooded Warbler (*Wilsonia citrina*)	0	1	0	0	2	7	3	0.04	0	1	0	0	9
Louisiana Waterthrush (*Seiurus moticilla*)	0	2	0	0	0	2	0	0	0	1	0	0	5
MacGillivray's Warbler[c,f] (*Oporornis tolmiei*)									0	5	0	0	5
Nashville Warbler[c,f] (*Vermivora ruficapilla*)	2	15	3	0.02					11	21	48	0.23	36
Northern Parula (*Parula americana*)	0	5	0	0					1	14	2	0.01	19
Northern Waterthrush (*Seiurus novaboracensis*)	0	10	0	0	0	5	0	0	0	5	0	0	20
Orange-crowned Warbler[c,f] (*Vermivora celata*)									4	10	15	0.15	10
Ovenbird (*Seiurus auricapillus*)	0	8	0	0	0	4	0	0	0	11	0	0	23
Palm Warbler (*Dendroica palmarum*)	0	12	0	0					0	15	0	0	27
Prairie Warbler (*D. discolor*)	0	2	0	0					1	11	1	0.01	13

TABLE 2. Continued.

	Nesting[a]				Fledgling[b]				Winter[c,d,e,f]				
Species	Calling periods	Total periods	Calls	Calls/ min	Calling periods	Total periods	Calls	Calls/ min	Calling periods	Total periods	Calls	Calls/ min	All Total periods
Wilson's Warbler[e,f] (*Wilsonia pusilla*)									0	8	0	0	8
Worm-eating Warbler (*Helmintheros vermivorus*)									1	5	0	0	5
Yellow Warbler (*Dendroica petechia*)	0	12	0	0					0	3	0	0	15
Yellow-rumped Warbler[c,e,f] (*D. coronata*)	0	19	0	0					0	12	0	0	31
Yellow-throated Warbler (*D. dominica*)									1	4	1	0.03	4
Totals	2	140	3	0.002	13	61	42	0.07	43	248	127	0.05	449

[a] Adirondacks and Finger Lakes, NY, USA 2003: 27 days, 140 observations, 1 Jun–14 Jul.
[b] Adirondacks and Finger Lakes, NY, USA 2004: 10 days, 61 observations, 1 Jul–1 Aug.
[c] Cuba 2004: 22 days, 189 observations, 31 Jan–27 Feb.
[d] Mexico 2003–04: 8 days, 18 observations, 27 Dec–2 Jan.
[e] Mexico 2004–05: 8 days, 17 observations, 27 Dec–3 Jan.
[f] Mexico 2005–06: 8 days, 24 observations, 27 Dec–7 Jan.

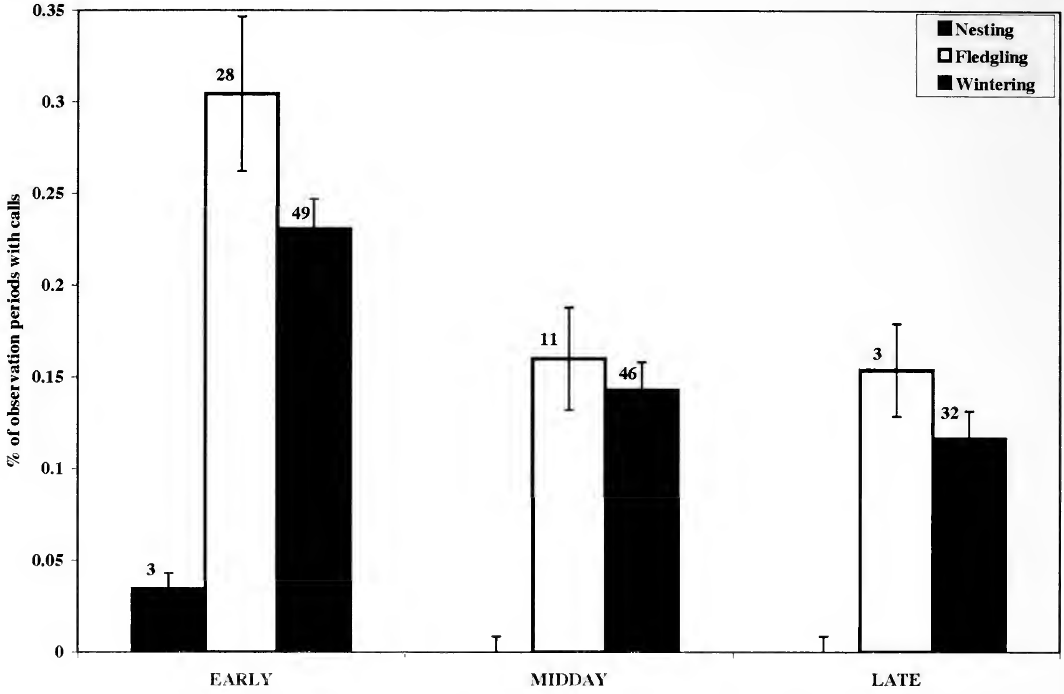

FIG. 3. Observation periods with warbler flight calls (%, x̄ ± SE) during nesting, fledgling, and wintering periods. Total flight calls recorded during the periods are shown above each histogram.

migration after the end of typical migration seasons (Terrill and Ohmart 1984, Terrill and Crawford 1988). However, this species rarely uses flight calls diurnally in place of its ubiquitous chip note. The Palm Warbler (*Dendroica palmarum*), which winters in large numbers in Cuba (Wilson 1996) and occasionally forms large flocks, follows a similar pattern in which birds do not use flight calls but instead use another call type ("chip" notes; A. Farnsworth, pers. obs.). The reasons behind this variation may relate to variation in flocking behaviors and are not yet understood. Examining facultative movements and details of flocking behaviors could yield additional information into the functions of flight calls.

Flight calls may also have longer-distance communication functions. Most birds, warblers included, vocalize extensively during nocturnal migration. Sounds travel greater distances at night (Larom 2002, Rundus and Hart 2002) and the distances that flight calls travel at night are likely substantially greater than those of calls during the day. In addition, flight calls of some species have frequency modulation (e.g., Cape May Warbler) that may facilitate localization. If flight calls facilitate grouping, regardless of the distances involved, a trade-off between localization by flock mates, communication of non-threatening intentions, and ventriloquy for predator avoidance may exist.

Non-migratory flight-calling could be an important behavioral component for understanding the evolution and ontogeny of these vocalizations. Research on specific behavioral contexts associated with flight calls is needed. Additional sampling of the annual cycle is also crucial. This research is especially important for examining the prevalence of flight calls during periods for which information is still scant (e.g., hatching period).

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FOOD SUPPLEMENTATION, TERRITORY ESTABLISHMENT, AND SONG IN THE PROTHONOTARY WARBLER

CHARLES E. CLARKSON[1]

ABSTRACT.—Bird song has been shown to be important in both inter- and intrasexual selection. Elaboration of the latter trait has been studied extensively. I conducted a field experiment to investigate the role of song in territory establishment of the Prothonotary Warbler (*Protonotaria citrea*). Songs were recorded for 31 males and song parameters were regressed against dates of territory acquisition, territory size, and territory location. In addition, feeders were placed in the territories of 17 randomly selected males. Song recordings from these males over the entire breeding season were compared with a reference group of 14 males. Males that sang more frequently acquired territories in preferred locations and earlier in the breeding season. A significant change occurred in song rate over the breeding season for males provided supplemental food. These findings suggest that physiological condition constrains song parameters that are important in territory establishment in the Prothonotary Warbler. *Received 19 July 2004. Accepted 9 October 2006.*

Bird song is a model system for the study of sexual selection (Andersson 1994, Nowicki and Searcy 2005). When attempting to decipher how sexual selection has shaped bird song, the constraints placed upon song production must be understood in the context of life history. Features such as breeding density, resource availability, and dispersal are important song performance predictors (Searcy and Andersson 1986). Further, constraints on bird song are likely to be different across species (Ritchison 1995, Oberweger and Goller 2001, Gil and Gahr 2002). For example, "performance-related" song traits, such as the amount of time a bird spends singing, have been hypothesized to involve physiological constraints (Gil and Gahr 2002; Nowicki and Searcy 2004, 2005). Changes in these song traits likely reflect changes in the physiological condition of a male. Therefore, males singing more frequently could be indicating the possession of a territory with high resource availability, as less time is necessary for foraging and more time can be devoted to territorial defense through song (Searcy and Andersson 1986, Strain and Mumme 1988, Nowicki and Searcy 2004).

Multiple studies have shown the importance of song in an intersexual context (Searcy and Andersson 1986, Andersson 1994); however, relatively few studies have examined song from an intrasexual context. The importance of song in territorial conflicts between conspecific males is difficult to study due to the presence of females. Questions regarding the importance of song in an intrasexual context are better investigated when territorial conflict occurs in the absence of females.

The objectives of my study were to examine: (1) if the ability of a male Prothonotary Warbler (*Protonotaria citrea*) to acquire a breeding territory is affected by song or some physical attribute, and (2) in an intrasexual context, is male physiological condition indicated through singing behavior?

METHODS

Study Species.—The Prothonotary Warbler is an ideal subject for study of song in relation to intrasexual selection theory as males arrive in breeding areas prior to females and compete with one another for nest sites (Petit 1989). Prothonotary Warblers readily use nest boxes and have been the subject of many studies on territory and nesting success (Petit et al. 1987, Petit 1989, Blem and Blem 1992, Petit and Petit 1996, Podlesak and Blem 2001). The significance of song in territory acquisition and defense by Prothonotary Warblers has not been examined (Shutler and Weatherhead 1990, Petit and Petit 1996).

Study Area.—This study was conducted from 14 April to 25 July 2004 within the 324-ha Dutch Gap Conservation Area, a brackish tidal swamp along the James River in Chesterfield, Virginia (37° 22′ N, 077° 30′ W). This site is part of a long-term Prothonotary Warbler study area extending from Curles Neck, Virginia to Presquile National Wildlife

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Refuge near Hopewell, Virginia. Approximately 100 numbered nest boxes were positioned an average of 97 m apart (range: 52–131 m) along the shoreline on both sides of a peninsula adjacent to the James River. Box heights ranged from 20 to 280 cm above the high tide line (Blem and Blem 1992). The boxes had been used by Prothonotary Warblers for approximately 4 years. The peninsula ranges in width from approximately 29 to 255 m. One side of the peninsula borders the James River and the opposite shoreline borders a tidal swamp with a number of islands dispersed throughout.

The habitat ranges from mid-succesional forest dominated by pine (*Pinus* spp.) and American holly (*Ilex opaca*), to periodically flooded areas dominated mainly by bald cypress (*Taxodium distichum*), green ash (*Fraxinus pennsylvanica*), red maple (*Acer rubrum*), and black gum (*Nyssa sylvatica*).

Song Recording, Territory Measurements, and Food Supplementation.—Males arrive as early as 3 April (Blem and Blem 1992) and I began checking the study site at 0400 hrs EST on 1 April to search for arriving males. The first males were detected on 12 April and began vocalizing on 14 April. Five minutes of continuous song were recorded as soon as males began singing each morning. Anywhere from three to five 5-min recordings were obtained for each male. I visually inspected sonograms of males to ensure that 5 min of song was sufficient to fully sample the variation within a song bout. I recorded all songs from 0500 to 0600 hrs using a Seinheisser shotgun microphone and a Marantz PMD221 portable cassette recorder. I ranked males according to the calendar dates on which they acquired their territories, based upon the dates when I initially detected their song. After a male's song was recorded, I captured the male by mist net, using taped song playbacks. I banded 57 males with a unique combination of colored leg bands and a Federal aluminum band, and recorded tail length (n = 57), wing chord length (n = 57), and mass (n = 23).

I mapped territory boundaries following Petit and Petit (1996) by following males for up to 3 hrs/day for 2 days. All points where males displayed signs of aggression (singing posts and defensive behavior in response to tape playback) were mapped using a Magellan Meridian Gold GPS unit. I superimposed the recorded waypoints onto a USGS quadrangle using Arcview GPS analysis software and calculated the area contained within the plotted waypoints. I designated territories as "1" if they bordered water and "2" if they did not.

I randomly selected 23 singing males to receive food supplementation for 4 weeks. The remaining 34 males received no supplementation and served as a reference group. I placed plastic cups containing commercially purchased waxworms (*Galleria mellonella*) (Morningdew Waxworm Supply Co., Trumansburg, NY, USA) within the territories of the supplemented warblers beginning on 27 April 2004 and observed the feeders daily to verify their use. The feeders were concealed by vegetation and I broadcasted conspecific song from a speaker placed near the feeder to initially attract the target male. Once the territorial male arrived to investigate, I used a remote signal to stop the recording. In most cases, the male warbler found the feeder and began feeding almost immediately. I filled all feeders on a daily basis with 30 g of waxworms. Any feeder not visited exclusively by the targeted male was excluded from the study.

Two weeks following the introduction of the feeders I recorded songs for all males in the study. Feeders were removed on 22 May and I resumed song recording beginning 4 June. This period provided males with a 2-week period to reduce potential carryover effects of food supplementation (Zar 1999). This recording pattern allowed me to sample initial songs from males as they acquired territories in the absence of females, songs from males whose physiological condition was altered through supplementary feeding, and songs following removal of the supplementation. Supplemental feeder use by birds other than the target male and difficulty in recording songs for some males for all three recording periods resulted in 31 complete data sets (17 supplemented, 14 unsupplemented).

Song Analysis.—I produced digital sonograms of songs using Raven Version 1.1 sound analysis software (Cornell University, Ithaca, NY, USA) with a sampling rate of 44,100 Hz (n = 225 songs from 31 males). I analyzed syllables from the best representative sonogram from each recording period for each male. I counted the number of syllables in each song bout over a 5-min period and made the following measurements on each syllable within a song bout: minimum frequency (Fmin) (Hz), maximum frequency (Fmax) (Hz), and Δ frequency (ΔF) (Hz) (n = 1,708 syllables). I also measured internote interval (ini) (sec) and syllable duration (syd) (sec). I divided the sum of syd for each song by duration of song to produce the proportion of on time, or the duration of each song bout in which the male is producing sound. I multiplied this proportion by 100 to yield the percent duty cycle (dc) (Thorson and Fine 2002). I recorded interbout intervals (ibi) (sec) for each 5 min of song.

Statistical Analyses.—I used a general linear model repeated-measures ANOVA (GLM, SPSS Version 11.5; 2002) to test for within-subjects (recording period) and between-subjects (supplemented vs. unsupplemented males) differences in song parameters. I used a repeated measures procedure since multiple measurements were obtained from each male during the study and independence of measurements could not be assumed (Zar 1999). I checked data for normality and sphericity prior to analysis and, where the assumption of sphericity was violated, I used Greenhouse-Geisser adjusted F-tests to interpret within-subjects effects (Burhans and Thompson 1998). I made repeated measures contrasts of within-subjects effects to identify which recording periods differed and t-tests to examine changes between subjects.

I used linear regression to test for correlations between pre-supplementation song parameters and physical measurements of the birds (wing chord, tail length, mass) upon arrival, as well as territory size and acquisition date. I used independent samples t-tests to examine differences in song in relation to territory location.

I performed all statistical analyses on SPSS Version 11.5 (2002). I checked all data for normality using Kolmogorov-Smirnov tests and visual inspection of histograms. Homoscedasticity was checked using Levene tests prior to analysis (dc did not violate the normality assumption and arcsin transformation did not lead to a difference in statistical results). Means are reported ± SE and I considered results significant if $P \leq 0.05$.

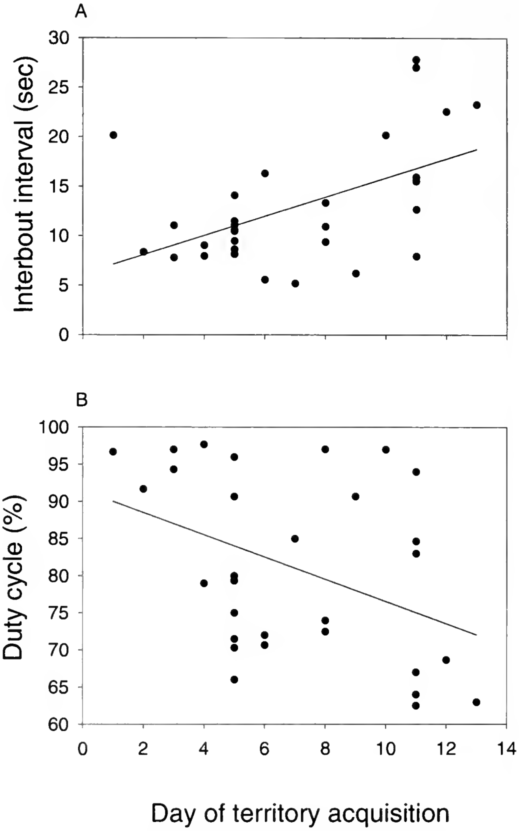

FIG. 1. (A) Interbout interval (sec) and (B) Duty cycle (%) as a function of day of territory acquisition in male Prothonotary Warblers.

RESULTS

Territory Acquisition and Male Physical Condition.—Birds which acquired territories earlier sang more frequently (had a shorter ibi) (n = 31, r^2 = 0.27, P = 0.003; Fig. 1A) and produced more sound (had a higher dc) (n = 31, r^2 = 0.15, P = 0 .012; Fig. 1B). Heavier birds and those with longer tails acquired territories earlier (tail length: n = 31, r^2 = 0.31, P = 0.001, Fig. 2A; body mass: n = 23, r^2 = 0.54, P < 0.001; Fig. 2B).

Average territory size for all birds was 0.26 ± 0.04 ha with a range of 0.02 to 0.71 ha (n = 31). Eighteen territories bordered water and 13 did not. No physical measurements or song measurements correlated with territory size; however, males establishing territories on the water sang more frequently (exhibited a significantly shorter ibi) (10.51 ± 0.76 sec) than

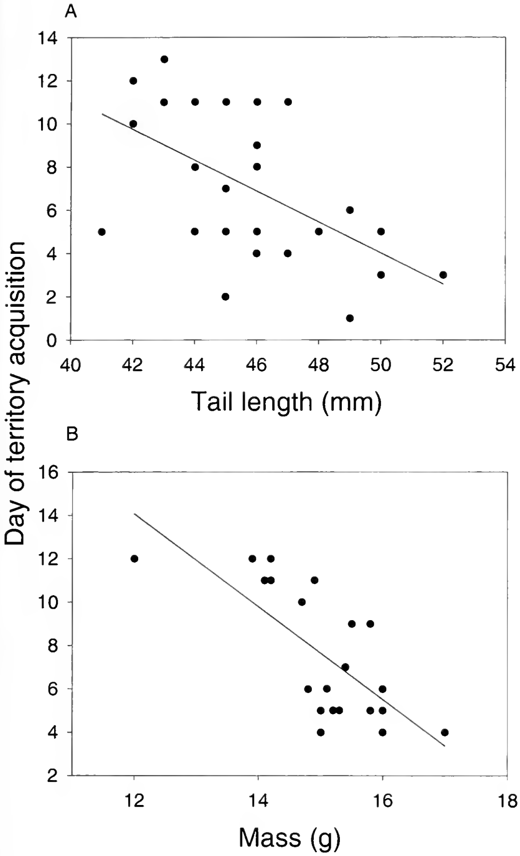

FIG. 2. (A) Tail length (mm) and (B) body mass (g) as a function of day of territory acquisition in male Prothonotary Warblers.

those inland (16.58 ± 2.26 sec) ($t = -2.55$; df = 29; $P < 0.001$; Fig. 3).

Effects of Food Supplementation.—Ninety-one sonograms were produced pre-supplementation, 65 during supplementation, and 69 post-supplementation. There were 1,708 syllables analyzed from these songs.

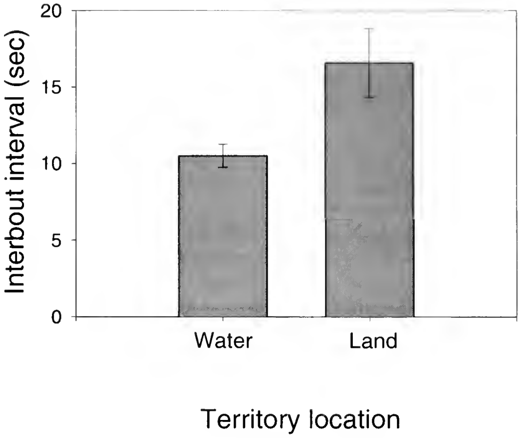

FIG. 3. Mean (± SE) interbout interval (sec) for male Prothonotary Warblers holding territories touching water (Water) and not touching water (Land).

A significant change in dc existed in both groups over the study period, although the groups did not differ in regard to percentage of time that sound was produced in a given song bout (within-subjects effects: F_{Adj}; = 11.64; $P = 0.000$; between-subjects effects: $F = 1.11$; $P = 0.30$) (Table 1). Within-subjects contrasts revealed a significant decrease in dc between the pre-supplementation and supplementation periods for both groups ($F = 12.75$; $P = 0.001$; Table 2, Fig. 4), but no significant difference between the supplementation and post-supplementation periods ($F = 0.05$; $P = 0.82$).

No significant within-subjects or between-subjects effects existed in ibi (within-subjects effects: $F = 0.90$; $P = 0.41$; between-subjects

TABLE 1. Changes in song parameters over a breeding season of Prothonotary Warblers. Significant results are represented by *.

	Within-subject		Between-subjects		Within · Between	
Song parameter	F	P	F	P	F	P
Duty cycle (%) (dc)	11.636*	0.000*	1.105	0.302	0.101	0.836
Inter-bout interval (ibi)	0.897	0.413	1.448	0.239	4.850*	0.011*
Song bout duration (sbd)	0.626	0.515	1.418	0.243	0.853	0.417
Maximum frequency	1.372	0.262	1.129	0.297	0.251	0.740
Minimum frequency	0.160	0.853	0.297	0.590	2.404	0.097
Δ Frequency	1.375	0.261	1.258	0.271	0.018	0.982
Syllable duration	2.961	0.060	0.165	0.687	0.130	0.878
Number of syllables	0.953	0.380	2.368	0.111	1.379	0.249

TABLE 2. Repeated measures analysis of variance for percent duty cycle (sec) (dc) over three song recording periods and within-subjects contrasts for male Prothonotary Warblers. Significant results are represented by *.

Source	df	SS	*F*	*P*
Within-subjects				
Period	1.418	1,650.325	11.636	0.000*
Period · Group	1.418	14.338	0.101	0.836
Between-subjects				
Group	1.000	32.285	1.105	0.302
Within-subjects contrasts[a]				
Period				
1 vs. 2	1.000	2,392.799	12.749	0.001*
2 vs. 3	1.000	2.676	0.052	0.820
Period · Group				
1 vs. 2	1.000	18.724	0.100	0.745
2 vs. 3	1.000	23.966	0.470	0.498

[a] Denotes pre-supplementation song recording (1), denotes during-supplementation song recording (2), and denotes post-supplementation song recording (3).

effects: $F = 1.45$; $P = 0.24$), yet a significant interaction existed between the two ($F = 4.85$; $P = 0.011$). Within-subjects contrasts found a significant difference in the interaction between the supplementation and post-supplementation periods ($F = 11.33$; $P = 0.002$; Table 3, Fig. 5). Supplemented males sang less frequently following the removal of feeders (an increase in ibi), while the frequency of song production did not change for unsupplemented males during the same period (paired samples *t*-test: $t = -3.011$; df = 16; $P < 0.05$, $t = 1.853$; df = 13; $P > 0.05$, respectively).

DISCUSSION

This experiment supports the hypothesis that song functions in territory acquisition in the Prothonotary Warbler, as song parameters recorded prior to the arrival of females correlated with both date of territory acquisition and territory location. In addition, the subsequent change in these song parameters following introduction and removal of supplemental food suggests that song in the Prothonotary Warbler is indicative of a male's current physiological condition.

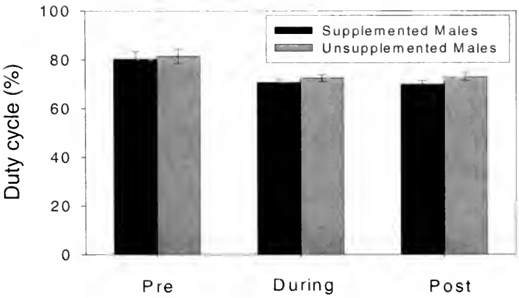

FIG. 4. Mean (± SE) duty cycle (%) in supplemented and unsupplemented male Prothonotary Warblers as a function of period ($n = 31$).

A tendency for earlier arriving male Prothonotary Warblers to exhibit a higher singing rate (larger dc and smaller ibi) is consistent with studies that documented higher singing rates and earlier arrival dates in dominant males (Yasukawa 1979, Read and Weary 1992, Duguay and Ritchison 1998, Lampe and Espmark 2003). The decline in dc and increase in ibi in males acquiring territories later in the breeding season may suggest these males are of poorer quality or less experienced than those arriving earlier. Larger body mass and tail length in early arriving males further suggests that dominant males are first to acquire a territory, as larger body size is likely to contribute to male dominance in Prothonotary Warblers (Petit and Petit 1996).

Territory Acquisition.—Petit and Petit (1996) examined territoriality in Prothonotary Warblers in relation to food availability, reproductive success, age, morphology, and plumage characteristics and found that territory partitioning follows the "ideal dominance" model (Fretwell and Lucas 1970). Dif-

TABLE 3. Repeated measures analysis of variance for interbout interval (ibi) over three song recording periods and within-subjects contrasts. Significant results are represented by *.

Source	df	SS	*F*	*P*
Within-subjects				
Period	2.000	61.114	0.897	0.413
Period · Group	2.000	330.355	4.850	0.011*
Between-subjects				
Group	1.000	69.685	1.448	0.239
Within-subjects contrasts[a]				
Period				
1 vs. 2	1.000	17.311	0.256	0.616
2 vs. 3	1.000	119.923	2.104	0.158
Period·Group				
1 vs. 2	1.000	87.427	1.295	0.264
2 vs. 3	1.000	645.701	11.330	0.002*

[a] Denotes pre-supplementation song recording (1), denotes during-supplementation song recording (2), and denotes post-supplementation song recording (3).

ferences in male quality result in the exclusion of subordinates from preferred habitat by dominant individuals (Petit and Petit 1996). Prothonotary Warblers prefer to nest over permanently inundated areas or areas that are periodically flooded (Walkinshaw 1953, Petit 1999), locations where predation risk and interspecifc competition are reduced (Petit and Petit 1996). Petit and Petit (1996) documented nonterritorial males throughout the breeding season despite multiple empty nest boxes in dry habitat and concluded this was likely the result of a lack of females willing to breed in an area where food availability is lower and predation pressure is increased. The results of my study are in accordance with those of Petit and Petit (1996) as male Prothonotary Warblers holding territories bordering water sang more frequently than males that nested inland. Time-spent singing (ibi) may therefore be an important indicator used by a male to assess the physiological condition of a rival during territory establishment. This is further supported by correlations between ibi and territory location prior to the presence of females or any period of territory tenure and likely reflects a male's physiological condition upon arrival in breeding areas.

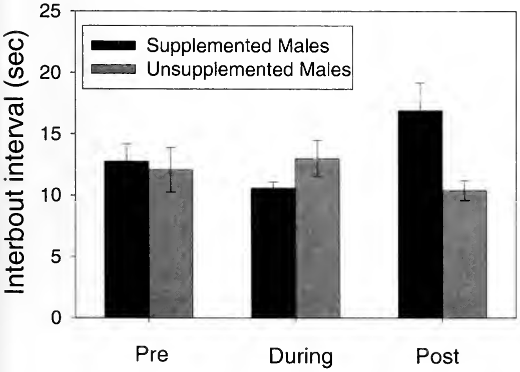

FIG. 5. Mean (± SE) interbout interval (sec) in supplemented and unsupplemented male Prothonotary Warblers as a function of supplementation period (n = 31).

A significant change in ibi between the two groups of males could be attributable to food supplementation. Following removal of supplemental food, a significant increase in ibi occurred for the supplemented males. Since ibi for unsupplemented males did not change significantly, this difference could be a direct result of feeder removal. Male warblers may have become dependent on supplementation as reflected in the significant increase in ibi by supplemented males following feeder removal. Previously supplemented birds may have decreased the amount of time they spent singing and increased foraging to meet energy demands previously provided by supplemental food.

A significant decline in dc for both groups of Prothonotary Warblers over the course of my study, with no significant change between groups, may be attributable to factors other than food supplementation. A significant decline in dc between the pre-supplementation and supplementation periods may suggest the establishment of a territory requires an increased rate of song, which has been previously noted in Prothonotary Warblers (Petit and Petit 1996). The absence of change in dc between the supplementation and post-supplementation periods may indicate that territory maintenance requires less singing effort than territory establishment. Initial song recordings may reflect competition for territory acquisition, while song recordings later in the breeding season may reflect maintenance of territories. Males may have been re-establishing tenure of territories that had already been acquired (Morse 1989, Ritchison 1995, Kroodsma 2004).

Song rate in Red-winged Blackbirds (*Agelaius phoeniceus*) differs between males establishing territories for the first time and males returning to re-establish territories during subsequent breeding seasons (Yasukawa 1979). Yasukawa (1979) found that males re-establishing territories in successive breeding seasons produced lower sound pressure level than males initiating a territory, suggesting that territory re-establishment is less costly than territory initiation (Yasukawa 1979, 1981; Picman 1987).

Dominance rank of Field Sparrows (*Spizella pusilla*) and Carolina Chickadees (*Poecile carolinensis*) during winter is associated with territory partitioning during the breeding season (Yasukawa 1979). It is therefore possible that certain song parameters indicate physiological condition in winter months in Prothonotary Warblers and are used to partition territories upon arrival in breeding areas. This hypothesis has not been tested in Prothonotary Warblers, but work by Marra et al. (1998) suggests that males in higher quality over-wintering habitat establish breeding territories earlier and are in better physiological condition.

Female Pied Flycatchers (*Ficedula hypoleuca*) choose males primarily on the quality of their territory (Alatalo et al. 1986). Male age, size, and song repertoire are not influential on female choice (Alatalo et al. 1986). Further, territory quality in *F. hypoleuca* is affected by arrival order to breeding areas with earlier arriving males singing longer songs (Lampe and Espmark 2003). Mate choice in Prothonotary Warblers could also be based on territory acquisition, which is dependent upon the frequency of song production and arrival order of males (Buchanan and Catchpole 1997). If true, females may be receiving direct benefits from mate choice in the form of resources (Buchanan and Catchpole 1997).

Darwin (1871) contended that one of the putative costs associated with singing is decreased survival through conspicuousness, which may be used to indicate both genetic and physiological vigor. The results of this experiment suggest the constraint associated with song used in the context of intrasexual selection by the Prothonotary Warbler is related to current physiological condition. The constraints on song production in terms of increased predation or intersexual selection are unknown as these were not measured in this study.

Certain song parameters and physical attributes of males were significant predictors of territory acquisition and partitioning in Prothonotary Warblers but were independent of one another. It is likely that territory acquisition and partitioning is governed by multiple interacting factors. For example, Petit and Petit (1996) suggest that body mass and plumage brightness in male Prothonotary Warblers likely has a role in territoriality; however, both measures are independent of age. Petit and Petit (1996) concluded that age also likely has an important role in territoriality. Until now, song has not been studied as a factor contributing to intrasexual competition in Prothonotary Warblers. The findings of this study should aid in examining the multiple factors associated with territoriality in this species.

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PROVISIONING RATES BY GOLDEN-WINGED WARBLERS

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ABSTRACT.—We studied parental provisioning rates and nestling body condition in an introgressed population of Golden-winged Warblers (*Vermivora chrysoptera*) in eastern Ontario. Twelve nests were monitored until the young fledged; six nests were parented by phenotypically pure Golden-winged Warbler males and females, and six were parented by pure Golden-winged Warbler males mated with introgressed hybrid females. Nestlings that had a hybrid parent did not show differences in body condition from nestlings with two Golden-winged Warbler parents. Provisioning patterns were examined for potential relationships with several different factors: gender of the parent (male vs. female), nestling age, pair type (pure vs. hybrid), and the proportion of extra-pair young in the brood. Both males and females increased their provisioning rates as nestlings grew, and males consistently provisioned at higher rates than females. Golden-winged Warbler parents and hybrid parents did not show significant differences in provisioning rates. Females significantly increased provisioning rates with increasing levels of extra-pair paternity. Our results suggest that hybrid nestlings are not at a disadvantage in terms of body condition, and that hybrid parents are equally adept at provisioning their young as are phenotypic Golden-winged Warbler parents. *Received 17 April 2006. Accepted 5 November 2006.*

Since their presumed split approximately 3 million years ago until recently, Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*Vermivora chrysoptera*) were geographically isolated (Gill 1980, 1997). Today, Blue-winged and Golden-winged warblers are sympatric and interbreeding in many areas of their respective breeding ranges; hybrid offspring are viable and readily backcross with both parental species (Parkes 1951). The recent decline of Golden-winged Warblers is associated with succession of shrub habitat into forest, and with hybridization and potential competition with the northward expanding Blue-winged Warbler (Confer et al. 2003). Predictable local extirpation of Golden-winged Warblers follows a brief period of hybridization; Blue-winged Warblers typically replace Golden-winged Warblers within 50 years of initial contact (Gill 1997). The future of the Golden-winged Warbler seems bleak because the number of allopatric Golden-winged Warbler populations continues to decline. It is likely the Golden-winged Warbler will become an extremely rare species, if not extinct, if the current trends of population decline continue (Gill 1980, 2004).

Several studies have examined hybrid fitness in the Golden-winged/ Blue-winged Warbler system. In central New York, Ficken and Ficken (1968a) reported preferential conspecific mating in areas of sympatry, which was accompanied by selection against male hybrids. They also found that interspecific pairings were relatively rare compared to pairings involving hybrids, a probable consequence of hybrid receptivity to both parental species (Ficken and Ficken 1968a). Similarly, Gill (1980) reported that hybrids in southern Connecticut obtain mates less readily than parental phenotypes. Hybrid pairs in a Pennsylvania population were found to have reduced reproductive success compared to pairs of phenotypically pure Golden-winged Warblers (Kubel 2005). These researchers observed that pairs involving a hybrid produced smaller clutches and had reduced hatching success when compared with pure pairs. Conversely, hybrid adults in eastern Ontario are just as likely to pair as pure warblers of either species relative to their abundance in the population, and hybrid nestlings are just as likely to fledge as pure Golden-winged nestlings (Vallender et al. 2007). In a large study of pairing success in New York, Confer and Larkin (1998) found that one of the most common hybrid pairings involve female hybrids backcrossed with Golden-winged Warbler males, consistent with our observations in eastern Ontario.

We investigated parental provisioning rates

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and nestling body condition in an introgressed Golden-winged Warbler population. We examined how each gender apportioned provisioning effort and how provisioning rates changed as nestlings matured. We also examined the relationship between paternity level and provisioning rates for both males and females, because Golden-winged Warblers follow a mixed reproductive strategy of social monogamy with genetic promiscuity via frequent extra-pair fertilizations (Vallender et al. 2007).

METHODS

Field research was conducted in May and June 2004 at the Queen's University Biological Station (QUBS), near Chaffey's Lock, Ontario, Canada (44° 34′ N, 76° 19′ W). Hybrids began breeding at QUBS within the past 10 years and Blue-winged Warblers within the past 2 years allowing us to study hybridization in its early stages. We classified each adult as Golden-winged Warbler, Blue-winged Warbler, "Brewster's Warbler", "Lawrence's Warbler" (the 2 recognized hybrid phenotypes; Parkes 1951), or introgressed. We classified individuals as introgressed if they displayed plumage that did not correspond with the parental or classic hybrid phenotypes described by Parkes (1951). Individuals with classic hybrid phenotypes as well as introgressed Golden-winged Warblers are hereafter referred to as "hybrids". Approximately 82% of the birds in our population were Golden-winged Warblers, 17% were hybrids, and 1% were Blue-winged Warblers. We captured males and females at focal nests using mist-nets and song playback, and assessed phenotypes upon capture. We measured mass and tarsus length, and collected blood samples using brachial venipuncture for genetic analysis. We banded adults with aluminum Canadian Wildlife Service bands as well as unique combinations of colored leg bands.

We monitored breeding pairs during nest building and egg laying. Nests of Golden-winged Warblers and their hybrids are difficult to find and we focused our intensive observations at a small number of nests. We banded nestlings at 4 days of age (day 1 = hatch day) with Canadian Wildlife Service bands, took measurements of mass and tarsus length, and collected small blood samples from the metatarsal vein.

We recorded parental provisioning at each nest for 6 consecutive days during the nestling period (days 3–8). Each day, for each nest, a 1-hr watch was recorded on video (n = 44 watches), or observed through binoculars from a nearby location (n = 16 watches). A Sony Hi8 Video Camera Recorder mounted on a tripod was used for video recording. We conducted watches between 1000 and 1400 hrs (EST) excluding the early morning period when males spend a considerable proportion of their time singing. We did not conduct watches during periods of rain, since provisioning rates are unusually low as females are constantly brooding; this reduced our number of watches from 72 to 60. Watch times were assigned so that, when logistically possible, a nest was observed in the late morning of one day, and then in the early afternoon of the following day.

We used four microsatellite loci, VeCr2, VeCr4, VeCr8, and VeCr14 (Stenzler et al. 2004) for parentage analysis and paternity assignment. These four loci offered a combined exclusion probability of 99.4%. We defined the social father as the male which was observed attending the nest. Offspring were considered to be extra-pair if their microsatellite genotype was mismatched with that of their social father. Full details of paternal assignment methodologies are in Vallender et al. (2007).

All statistical analyses were performed using JMP v. 5.1 (SAS Institute 2005). We calculated a nestling body condition index using the residuals of a regression of mass over tarsus length (Jakob et al. 1996). We performed REML mixed model regressions to compare nestling body condition by pair type (pure vs. hybrid). We partitioned our analyses because 11 of 12 of nests (92%) contained young produced as a result of extra-pair copulations involving a male other than the social father and 40% of all nestlings (23 of 57) were extra-pair young. We first included within-pair offspring only, so the phenotype of both genetic parents was known, and then repeated our analysis for all young in the nests. Brood was used as a random effect and pair type as a factor to examine if there were differences in body condition of nestlings provisioned by pure parents and those provisioned by hybrid parents.

We quantified parental provisioning separately for males and females, and calculated hourly provisioning rates (trips/nestling/hr) to compare levels of parental provisioning. We used standard transformations to improve the normality of provisioning data and ensured residuals were normal. Transformed provisioning values are used in all analyses. We performed an EMS mixed model regression to test for the effects of gender of the parent, nestling age, pair type, and all appropriate two-way interactions on provisioning rates. We included brood as a random effect to control for repeated observations at the same nests, allowing us to treat each observation as an independent data point.

We tested for a relationship between the proportion of extra-pair young in broods and provisioning rates. We used the residuals of a regression of provisioning rate and nestling age to control for the significant effect of nestling age on provisioning rates for this analysis. We calculated a mean value for each individual parent and examined the relationship between mean provisioning rate and the proportion of extra-pair young in the nest for each gender.

RESULTS

Our observations of parental care focused on six nests of phenotypically pure Golden-winged Warbler males mated with phenotypically pure Golden-winged Warbler females, hereafter referred to as "pure nests", and six nests of phenotypically pure Golden-winged Warbler males mated with introgressed hybrid females, hereafter referred to as "hybrid nests". All hybrid females were classified as introgressed, resembling the Golden-winged Warbler phenotype but with a characteristic yellow wash, reminiscent of "Lawrence's" Warblers. We were unaware of any nests parented by Blue-winged Warblers. Brood size ranged from three to six young (mean ± SE = 4.75 ± 0.25); excluding one known re-nest, average clutch size for pure pairs was 5.0 young and for hybrid pairs was 4.8 young. The first egg date for pure pairs occurred between 4 June and 24 June 2005; the first egg date for hybrid pairs occurred during the same period between 4 June and 23 June 2005.

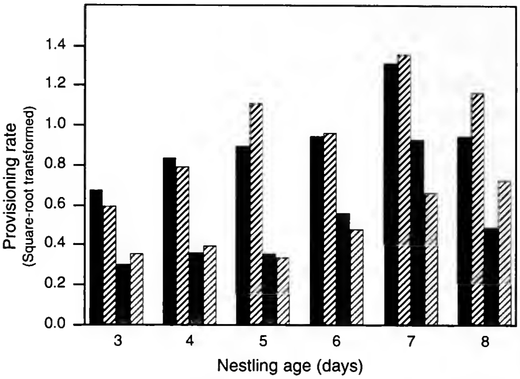

FIG. 1. Provisioning rates of male and female Golden-winged Warblers and hybrids as nestlings mature (provisioning trips/nestling/hr). Males paired with pure Golden-winged females (■) provision at similar rates to males paired with hybrid females (▨), and pure Golden-winged Warbler females (■) provision at similar rates to hybrid females (▨). Both males and females increase provisioning rates as nestlings grow older, with males consistently provisioning more often than females.

Nestlings that had two pure Golden-winged Warbler parents did not show differences in body condition from nestlings with a hybrid parent. This was true when the analysis included only within-pair young (overall model: $r^2 = 0.18$, $F_{10,23} = 0.71$, $P = 0.70$; pair type: $F_{1,23} = 1.28$, $P = 0.27$; brood: $F_{9,23} = 0.51$, $P = 0.85$) and when all nestlings were included (overall model: $r^2 = 0.16$, $F_{11,45} = 0.97$, $P = 0.49$; pair type: $F_{1,45} = 1.20$, $P = 0.28$; brood: $F_{10,45} = 0.83$, $P = 0.60$).

Mixed model regression (REML) showed there was no effect of time of day on provisioning rate (overall model: $r^2 = 0.35$, $F_{12,47} = 2.11$, $P = 0.034$; time of day: $F_{1,47} = 1.86$, $P = 0.18$; brood: $F_{11,47} = 2.04$, $P = 0.045$); consequently we pooled morning and afternoon observations for subsequent analyses. Our EMS model revealed that provisioning rate was influenced by gender of the parent, nestling age, and brood, but not pair type (overall model: $r^2 = 0.66$, $F_{15,104} = 13.29$, $P < 0.0001$; gender of the parent: $F_{1,104} = 49.74$, $P < 0.0001$; nestling age: $F_{1,104} = 44.05$, $P < 0.0001$; brood: $F_{11,104} = 3.81$, $P = 0.0001$; pair type: $F_{1,104} = 0.67$, $P = 0.41$; Fig. 1). No two-way interactions were significant. Thus, we found that males provisioned significantly more than females and that hybrid and pure Golden-winged Warblers provisioned at similar rates throughout the nestling period (Fig. 1).

Females significantly increased provisioning rates with increasing levels of extra-pair paternity ($r^2 = 0.46$, $F_{1,10} = 8.68$, $P = 0.01$). Male provisioning rate was unrelated to paternity level ($r^2 = 0.17$, $F_{1,10} = 2.02$, $P = 0.19$).

DISCUSSION

Nestling provisioning by males and females in our introgressed Golden-winged Warbler population followed a similar pattern as nestlings developed. Both males and females significantly increased their provisioning rates as nestlings matured, with males assuming a larger role in nestling provisioning than females (Fig. 1). This result is unusual for a passerine, since most species show near equality of provisioning effort (Breitwisch et al. 1986). Greater provisioning rate by males is especially unusual for a warbler species, given that many warblers have role equality or higher rates by females. For example, Nolan (1978) reported that male and female Prairie Warblers (*Dendroica discolor*) provision nestlings at similar rates, although females provision slightly more often than males. Near equal division of provisioning labor also occurs by the Black-throated Blue Warbler (*D. caerulescens*; Chuang-Dobbs et al. 2001) and the Nashville Warbler (*Vermivora ruficapilla*; Knapton 1984). Female Yellow Warblers (*D. petechia*) consistently provision young more often than males (Yezerinac et al. 1996).

The higher provisioning rate by male Golden-winged Warblers (Fig. 1) may be due to strong predation pressure, as this species nests on the ground where nestlings are easily accessible to a suite of predators. Golden-winged Warblers have a shorter nestling period (8–9 days; Confer 1992) than other warbler species that do not nest on the ground (e.g., 9 days for the Black-throated Blue Warbler [Chuang-Dobbs et al. 2001] and 10 days for the Yellow Warbler [Knapton 1984]). Increased provisioning by males reduces the time that nestlings are vulnerable to predation in the nest (Breitwisch et al. 1986). Once nestlings are able to thermoregulate, females do not need to spend as much time brooding and would be expected to increase provisioning rate. However, females need to replenish their own depleted stores after 2 weeks of incubating eggs and brooding hatchlings (Moreno 1989). Thus, females may be subject to physiological constraints which impose an upper limit on their provisioning effort.

Pure Golden-winged Warbler and hybrid pairs were equally adept at provisioning their young as pair type did not influence provisioning rate (Fig. 1). Thus, hybrid pairs appear just as capable of producing viable young and successfully rearing them to fledging as pure pairs. Furthermore, in a 4-year study of this population, Vallender et al. (2007) found that hybrid adults do not produce smaller clutches nor fledge fewer young than their pure counterparts, and that hybrids are just as likely to pair as are phenotypic Golden-winged Warblers relative to their abundance in the population. Our study reveals that female hybrids achieve similar reproductive success to phenotypic Golden-winged Warblers.

Females significantly increased provisioning rate with increased extra-pair paternity level, but there was no relationship between male provisioning and paternity level. A female may gain genetic diversity or superior male genes or both for her offspring by mating with multiple males (Tregenza and Wedell 2000); a brood of mixed paternity may therefore be considered more valuable to a female. Like Golden-winged Warblers, Black-throated Blue Warbler females increase parental care with extra-pair fertilizations (Chuang-Dobbs et al. 2001). The relationship between paternity and male parental care varies among species because of variation in paternity cues available to males, and the costs and benefits of reducing care (Whittingham and Dunn 2001). The absence of reliable cues may prevent males from facultatively adjusting their paternal care. In the Yellow Warbler, males had low accuracy in assessing their parentage, as they were incapable of distinguishing kin from non-kin at the nest (Yezerinac et al. 1996). In the Eastern Bluebird (*Sialia sialis*), paternity had no effect on male provisioning rate, suggesting that males may tolerate the possibility of paternity reduction if paternal care is crucial to nestling survival (MacDougall-Shackleton and Robertson 1998).

There was no difference in body condition between nestlings raised by hybrids and those raised by pure Golden-winged Warbler parents. Similarly, hybrid pairs appear equally adept at producing and fledging young as pure pairs, suggesting that hybrid parents are not of lower quality. Hybridization has been suggested as a mechanism by which Blue-winged Warblers replace Golden-winged Warblers, but the details are largely unknown (Confer et al. 2003). Our study contributes to our understanding of the dynamics of this hybrid zone by showing that female hybrids are equally successful parents as pure Golden-winged Warblers. Our findings suggest that, at least at the nestling stage, hybrids are not at a disadvantage. Negative effects of hybridization may be realized after the nestling stage; males may act as a genetic sieve due to female choice for optimal males (Houle and Kondrashov 2002). Adult hybrid males do appear to suffer in terms of reproductive success compared to phenotypic Golden-winged Warbler males in several areas of the hybrid zone (Ficken and Ficken 1968b, Confer and Larkin 1998, Kubel 2005). However, several lines of evidence indicate that, in our population, the reproductive success of hybrids does not appear to be less than phenotypically rare Golden-winged Warblers (Vallender et al. 2007). This is likely one reason why hybrid numbers have increased dramatically in past years. If similar processes operate across the hybrid zone, Golden-winged Warblers are likely to continue to decline and their fate to remain uncertain.

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PROVISIONING OF YOUNG BY THE ORIENTAL MAGPIE-ROBIN (*COPSYCHUS SAULARIS*)

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ABSTRACT.—Information on provisioning behavior of birds in the Indian subcontinent is almost negligible. We studied provisioning of nestlings of the Oriental Magpie-robin (*Copsychus saularis*) in 11 nests in relation to brood size, nestling age, and time of day during March–July 2006. Both parents fed the nestlings. However, the rate of provisioning trips by females was higher (t = 9.51, df = 10, $P < 0.01$) than for males. Brood size and time of day did not affect the provisioning rate. Age of nestlings was an important factor affecting rate of parental provisioning. Nestlings were fed more as they became older and there was correlation (Spearman's rho = 1) between parental provisioning trips and nestling age. *Received 10 August 2006. Accepted 30 November 2006.*

Successful production of young is an essential component of individual fitness (Stearns 1992) as well as being crucial to maintenance of population levels (Nolan 1978, Virolainen 1984, Sherry and Holmes 1992, Holmes et al. 1992). Socially monogamous, biparental passerines expend considerable effort in parental care that includes nest building, incubation, food provisioning, vigilance, and brooding (Skutch 1976, Breitwisch 1989, Clutton-Brock 1991). However, these efforts may be energy-demanding and potentially risky to survival of the parents and their lifetime reproductive success (Curio 1988).

Predation has been assumed to be the single most important factor affecting breeding success of most passerine birds (Holmes et al. 1992, Martin 1992a). However, parental care may be more important. For example, quantity of food delivered can influence nestling survival as measured by brood reduction due to starvation in many passerine birds (Magrath 1990) and by starvation of entire broods (Sherry and Holmes 1992). Young can also attract predators by their loud begging calls, if not fed well, which may lead to nest loss from predation (Skutch 1949, Martin 1992b).

Studies have indicated that parental contribution in terms of provisioning rates can be influenced by the demands of the nestlings (i.e., brood size, nestling age) and/or by environmental factors (e.g., weather conditions, time of season, time of day) (Royama 1966, Seel 1969, Best 1977, Pinkowski 1978, Johnson and Best 1982, Bedard and Meunier 1983).

The objectives of our study were to: (1) document provisioning patterns of male and female Oriental Magpie-robins (*Copsychus saularis*), and (2) compare these patterns to brood size, nestling age, and time of day.

The Oriental Magpie-robin is a dichromatic, insectivorous, hole-nesting species (Ali and Ripley 1998) which selects natural tree cavities in a variety of trees including *Pyrus communis*, *Mangifera indica*, *Eriobotrya japonica*, and *Moringa oleifera*. It breeds during the summer/monsoon season. Eggs are laid at the interval of one/day and 4–5 eggs is the usual clutch size (Ali and Ripley 1998). Both parents feed the young, mainly with insect larvae, and the average nestling period is 14.0 ± 0.4 days (DB and VKS, unpubl. data).

METHODS

The study was conducted in the Himalayan foothills at Haridwar (29° 55′ N, 78° 08′ E), Uttaranchal (UA), India from 5 March to 20 July 2006. Systematic searches were made in suburban habitats during morning and evening to locate nests. Sixteen nests were discovered, three during building, nine during egg laying, and four during incubation. All nests were inspected daily. Three nests were predated during incubation and two during the third and seventh day post hatching. These five depredated nests were excluded from the analysis. Thus, data were collected from 11 nests during the nestling period.

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TABLE 1. Comparative provisioning trips/hr for 11 pairs of Oriental Magpie-robins.

	Average provisioning trips/hr			
Pair	Male	Female	M + F	Brood size
1	6.19	6.8	12.99	4
2	5.47	8.09	13.56	4
3	5.66	7.47	13.13	4
4	5.8	8.66	14.46	4
5	5.95	7.57	13.52	4
6	5.09	8.28	13.37	4
7	5.8	8.14	13.94	4
8	6.42	8.28	14.7	5
9	5.42	8.19	13.61	5
10	5.71	7.28	12.99	5
11	5.8	7.8	13.6	5
MEAN	5.8	8.1	13.5	
SD	0.4	0.5	0.5	

Parental provisioning rates were measured by observing nests from a distance of 30–90 m from a blind with 7 × 50 binoculars. Parents were observed as they approached nest cavities with food in their bill and fed the nestlings. We counted this event as a single provisioning trip. Each observation period was 1 hr in length and each day was divided into three periods: 0600–0800 hrs (morning), 1230–1430 hrs (afternoon), and 1700–1900 hrs (evening). Food items infrequently projected beyond the margins of the bills of adults. Therefore, prey size identification was not possible and this parameter was excluded. Data were not collected during rain since rainfall may affect provisioning rate by extending brooding time (Johnson and Best 1982). Data were analysed statistically using Spearman's rho correlation and paired sample *t*-tests (Baily 1995).

RESULTS

We recorded 3,178 provisioning trips by both parents at the 11 nests during the present study. The provisioning rate for females was 8.1 ± 0.5 (SD) trips/hr and 5.8 ± 0.3 trips/hr for males (Table 1). Female Oriental Magpie-robins had significantly ($t = 9.51$, df = 10, $P < 0.01$) more provisioning trips to nestlings (58.2%) than males (41.8%).

Seven of 11 nests had four nestlings and four had five nestlings. Males averaged 5.8 ± 0.3 (SD) and 5.7 ± 0.4 trips/hr to nests containing four and five nestlings, respectively. Corresponding figures for the females were 8.1 ± 0.6 and 8.0 ± 0.4 trips/hr. Brood size had no effect on parental feeding rates ($t = 0.350$, df = 3, ns). However, each young in nests containing five nestlings received fewer provisioning trips than those in nests with four nestlings.

Nestlings were fed more as they became older and there was a correlation between parental provisioning trips and nestling age (Spearman's rho = 1). Provisioning trips of females increased progressively throughout the nestling period (Fig. 1). Males made more trips than females during the first and third days of the nestling period ($t = 4.99$, df = 32, $P < 0.01$ for day 1 and $t = 4.10$, df = 32, P

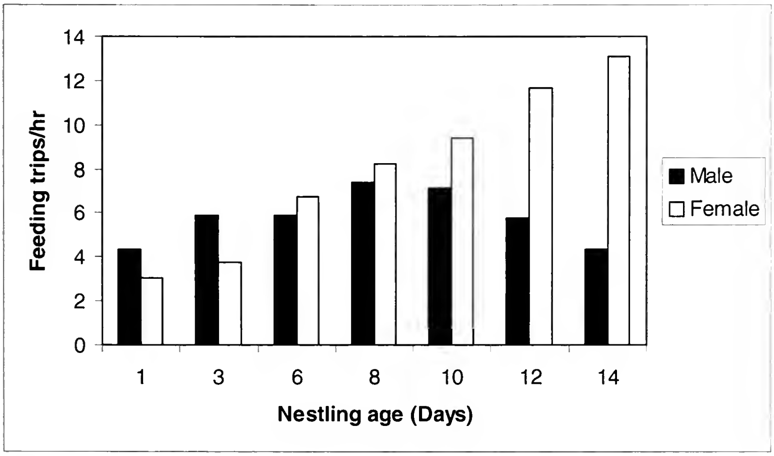

FIG. 1. Effect of nestling age on provisioning rate of the Oriental Magpie-robin.

TABLE 2. Average provisioning trips/hr in relation to time of day and nestling age of Oriental Magpie-robins.

Nestling age (days)	Provisioning trips/hr		
	Morning	Afternoon	Evening
1	7.63	7.18	7.35
3	9.72	9.17	8.62
6	12.44	12.71	12.81
8	16.45	14.71	15.53
10	15.27	15.9	18.45
12	18.18	16.99	17.17
14	17.17	17.99	17.36

< 0.01 for day 3). Females fed more often than males in the later days ($t = 2.37$, df $= 4$, $P < 0.01$). Fewer trips of females in relation to males during the first and third days were probably the result of their involvement in brooding. Females spent more time in nest cavities (for brooding) during the early hatchling period (32.2 ± 4.2 min/hr, $n = 9$, day 1 of nestling age) and this time decreased with nestling age (26.2 ± 2.1 min/hr, $n = 7$ on day 3, 18.1 ± 2.2 min/hr, $n = 8$ on day 6, and only occasionally thereafter). Males were not observed to remain in nest cavities. Males showed an increase in trips up to 8 days of age of the nestlings with a slight decrease on day 10 and significant declines following days 12 and 14 (Fig. 1).

There was no significant variation in number of parental provisioning trips during the morning, afternoon, and evening. Thus, time of day did not affect provisioning rates of Oriental Magpie-robins as parents fed nestlings at almost the same rate at different parts of the day (Table 2: $t = 0.881$, df $= 6$, ns for morning vs. afternoon; $t = 0.109$, df $= 6$, ns for morning vs. evening; $t = 0.927$, df $= 6$, ns for afternoon vs. evening).

DISCUSSION

Our results clearly indicated that provisioning trips by female Oriental Magpie-robins were significantly higher than for males. This was probably due to greater involvement of males in nest guarding. However, relative role of males and females in provisioning young varies among species with no consistent pattern (Goodbred and Holmes 1996). Females of some species have been reported providing more food to the nestlings than males (Nolan 1978, Pinkowski 1978), while in others, males provide more food (Biermann and Sealy 1982, Johnson and Best 1982, Tamatha and Breitwisch 1997). In some species both parents feed nestlings at similar rates (Best 1977, Nolan 1978, Knapton 1984, Breitwisch et al. 1986, Dittami et al. 1991, Conard and Robertson 1993, Cooper and Ritchison 2005).

Feeding rates generally increase with an increase in brood size (Lack and Silva 1949, Royama 1966, Morehouse and Brewer 1968, Best 1977, Johnson and Best 1982). However, in our present study, provisioning trips of Oriental Magpie-robins were not affected by brood size. Pinkowski (1978) also reported no positive relation between brood size and feeding rate by either male or female Eastern Bluebirds (*Sialia sialis*). Other investigators have also found similar trends for House Sparrow (*Passer domesticus*) (Seel 1969), Savannah Sparrow (*Passerculus sandwichensis*) (Bedard and Meunier 1983), Nashville Warbler (*Vermivora ruficapilla*) (Knapton 1984), Northern Mockingbird (*Mimus polyglottos*) (Breitwisch et al. 1986), and Western Bluebird (*Sialia mexicana*) (With and Balda 1990).

The positive relationship between nestling age and number of provisioning trips for Oriental Magpie-robins is probably related to increasing energy demands of the young. This pattern has been reported for other avian species as well (e.g., Morehouse and Brewer 1968, Nolan 1978, Biermann and Sealy 1982, Johnson and Best 1982, Bedard and Meunier 1983, Breitwisch et al. 1986, Haggerty 1992). However, feeding rates of Yellow-breasted Chats (*Icteria virens*) (Schadd and Ritchison 1998) and Nashville Warblers (Knapton 1984) did not vary with nestling age.

We did not find any diurnal variation in parental provisioning trips of Oriental Magpie-robins. This species is a summer/monsoon breeder that feeds young mainly with insect larvae available within its territory. Parents provisioned the young frequently with almost constant speed throughout the day, probably because of the easy accessibility and small sizes of food items. Time of day has been reported as having no effect on food provisioning in other species (e.g., Black-throated Blue Warbler [*Dendroica caerulescens*] [Goodbred and Holmes 1996], Yellow Warbler [*D. petechia*] [Biermann and Sealy 1982], and Bachman's Sparrow [*Aimophila aestivalis*] [Haggerty 1992]). However, Nolan (1978) reported some variation in foraging rate during the day for the Prairie Warbler (*Dendroica discolor*) with an increase in the morning shortly after dawn and a smaller increase late in the day. More pronounced diurnal patterns have been reported for Eastern Kingbirds (*Tyrannus tyrannus*) (Morehouse and Brewer 1968), Eastern Bluebirds (Pinkowski 1978), and Nashville Warblers (Knapton 1984) for which provisioning rates decreased in the middle of the day and increased later in the day.

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WINTERING DISTRIBUTIONS AND MIGRATION OF SALTMARSH AND NELSON'S SHARP-TAILED SPARROWS

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ABSTRACT.—We delineate the winter distributions of the five subspecies of Saltmarsh Sharp-tailed (*Ammodramus caudacutus*) and Nelson's Sharp-tailed (*A. nelsoni*) sparrows, and comment on patterns of migration. The two subspecies of *A. caudacutus* (*A. c. caudacutus*, *A. c. diversus*) have similar core winter ranges that extend along the Atlantic coast from North Carolina to northeastern Florida. They also occupy two isolated areas within peninsular Florida in Everglades National Park and on the northwest Gulf coast. Migration in *A. caudacutus* is mainly confined to the coast. The subspecies of *A. nelsoni* (*A. n. nelsoni*, *A. n. alterus*, *A. n. subvirgatus*) occupy different but overlapping winter ranges. *A. n. nelsoni* is the most widespread, occurring from North Carolina to Texas. Some birds migrate along the Atlantic coast southwards in fall, and others follow interior routes through the Mississippi River watershed in both fall and spring. We suggest *A. n. nelsoni* wintering along the Atlantic coast in spring fly directly inland towards their northern breeding areas. Some birds in fall also approach the southeastern coastline directly across the Appalachian Mountains. *A. n. alterus* mainly winters along the southeastern Atlantic coast to Florida, and in fewer numbers along the Gulf coast at least to Louisiana. Some *A. n. alterus* may migrate to the Gulf coast directly via inland routes west of the Appalachian Mountains. *A. n. subvirgatus* has the most limited wintering distribution, from South Carolina to northeast Florida, and is strictly a coastal migrant south of New England. Limited wintering ranges and narrow winter habitat requirements place continental populations of sharp-tailed sparrows at risk. *Received 30 November 2005. Accepted 31 August 2006.*

Breeding populations of sharp-tailed sparrows are distributed in three discrete regions of mostly once-glaciated North America. For nearly 65 years these sparrows were treated as a single species (AOU 1931). Recently, new information on social behavior and genetics led to a re-split of this complex into two polytypic species (Greenlaw 1993, Rising and Avise 1993, AOU 1995). The southern Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*; hereinafter Saltmarsh Sparrow) has two subspecies, *A. c. caudacutus* (coastal breeding, Maine to New Jersey) and *A. c. diversus* (coastal, New Jersey to Virginia). The northern Nelson's Sharp-tailed Sparrow (*A. nelsoni*; hereinafter, Nelson's Sparrow) has three subspecies, *A. n. nelsoni* (breeds in northern Great Plains), *A. n. alterus* (James Bay north to Churchill, Manitoba), and *A. n. subvirgatus* (coastal, Québec to northeastern Massachusetts). The breeding distributions of the two species and their respective subspecies are well known (Greenlaw and Rising 1994, Hodgman et al. 2002), but their wintering ranges are poorly understood (Greenlaw and Rising 1994, Post 1998). In addition, much remains to be learned about migration in the two species. We examined over 1,000 specimens of sharp-tailed sparrows, mostly taken along the Atlantic and Gulf coasts of the United States during the post-breeding period, and independently assigned them to subspecies using a synoptic key that we developed. We provide specimen-based information on wintering distributions of the subspecies and on migration chronology in different coastal regions, and comment on inferred routes of migratory travel. We also consider the conservation implications of our findings.

METHODS

This study is based on review of specimens in 28 collections in the United States. Initially, we examined a series of 191 specimens of sharp-tailed sparrows from the five different breeding areas, and devised a dichotomous key to the species and subspecies in the complex (Appendix 1). We used a suite of plumage characters and bill length (anterior nares to tip of maxilla, measured by calipers to nearest 0.1 mm) to devise a series of hierarchically arranged couplets in the key. Each plumage character in the couplets has two divergent character choices, each of which represents variations that are characteristic of a particular

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taxon. These divergent character choices represent the endpoints of an implied gradient. JSG (unpubl. data) originally identified these gradients using voucher specimens to represent variation within and among taxa along an arbitrary ordinal scale for each focal character. Confidence of diagnosis in using the key is high if all or most of the characteristics in a set of couplet paragraphs match a given specimen. The key assigns a specimen to a species or subspecies. However, observed character expressions may fall between the contrasting variations most representative of the two taxa identified in a couplet (intermediate variations). Variations of different focal characters in some instances may be closest to one or the other of two taxa keyed by a couplet, but do not conform in identifying a single taxon (mosaic occurrence of variations). We treated specimens in these cases as intergrades (e.g., *A. n. nelsoni/alterus*). The few hybrids were similarly identified at the species-level couplet. JSG had previously examined hybrids from Maine between the two species and had experience with character expression in these specimens (Greenlaw 1993).

We examined 970 non-breeding specimens from coastal sites that were potentially within the primary wintering ranges of the two species (Maryland to Texas). We also examined eight winter specimens taken along the coast in New York and Massachusetts, and a few migrants from continental interior (n = 12), subcoastal (12), and Appalachian Mountain (3) localities. Overall, we processed 1,005 specimens from most Atlantic and Gulf coastal areas in the United States, and a few inland sites, covering the period from September through May 1869–2002.

Our analyses mainly focused on species and subspecies composition among coastal states during the non-breeding seasons specified as winter, December through March; fall migration, September through November; and spring migration, April and May. Migration of sharp-tailed sparrows is essentially over by mid-November, and does not begin in the spring until after molt ends in early April (Greenlaw and Rising 1994). We restricted our analysis of "wintering" birds to winter-season specimens only along the Atlantic coast south to Georgia where through-migration (transients) occurs in fall and spring. We regarded all specimens from earliest arrivals (Sep) to the last departures (May) to represent "wintering" in the southernmost states (Florida to Texas) where through-migration ceased. We recognized four subregions in Florida: northeast (Nassau County south to Martin County), south (Palm Beach and Charlotte counties southward), northwest (Wakulla County south to Sarasota County), and panhandle (Franklin County westward). All specimens from the Florida panhandle proved to be *A. n. nelsoni*; thus we treated this subregion as part of a larger northern "Gulf" region (Florida panhandle to Texas) in which the nominate subspecies predominated. Our maps show specimen occurrence at the county or parish level within states, regions, or subregions and we provide a detailed summary matrix of our coastal data on non-breeding sharp-tailed sparrows (Appendix 2).

JSG and GEW evaluated each non-breeding specimen independently, and assigned species and subspecies in each case. Measurements taken were wing chord (to nearest 0.5 mm) and bill length. Plumage color and pattern were assessed using the synoptic key, and were not scored. We did not detect any evidence of fading in plumage colors we used in our key based on specimen age. We compared specimens by subspecies, season, gender, and age collected in the late nineteenth century versus those taken in the mid- and late twentieth century. Feather wear was a factor of some concern because it especially affects the buffy, ocher, and orange hues on the sides of the head and breast. We found that hue contrasts between feather regions (e.g., malar region vs. breast) tended to be maintained (or sometimes were exaggerated in the case of differential wear) in worn versus fresh-plumaged specimens. All information was placed in an electronic data base where it could be selectively queried. We used only the assignments on which we agreed. Assignment conflicts and intergrades between subspecies were excluded from consideration. We agreed on all species-level identifications. However, our species assignments differed from those of an earlier authority in 3% of the specimens examined (n = 31). These were instances of Nelson's Sparrows that were mistakenly identified as Saltmarsh Sparrows, probably because of heavy ventral streaking (Howell and Sibley 1998).

We concurred on 91% of all our subspecies assignments. Thus, our error rate between investigators in this key-based method was 9%. This method, in which two people independently diagnosed subspecies, allowed us to identify and exclude non-conforming identifications from our analyses. We believe the key is reasonably accurate in identifying specimens of *A. n. subvirgatus*, and typical specimens of *A. n. alterus* and *A. c. caudacutus*. We interpreted plumage variation in *A. n. nelsoni* and in *A. c. alterus* in such a way that the key likely assigns bright, strongly flank-streaked variants of *A. n. alterus* to *A. n. nelsoni*, and the darkest variants of *A. c. caudacutus* to *A. c. diversus*. Thus, our data may over-represent *A. n. nelsoni* versus *A. n. alterus*, and *A. c. diversus* versus *A. c. caudacutus*.

We analyzed frequency data arrayed in two-way (row [subspecies] × column [region or subregion]) tables. Goodness-of-fit tests for independent samples are appropriate for discrete frequencies in nominal categories. We asked whether frequency distributions of wintering sharp-tailed sparrows, represented as specimens, were random samples taken from a single, homogeneous wintering community of species and subspecies among and within (Florida only) states. We used the Likelihood Ratio Test in our analyses (Sokal and Rohlf 2000). We followed the convention recommended by Sokal and Rohlf (2000: 696) of labeling the sample statistic X^2 rather than X^2. We initially evaluated data across all states or groups of states and then pooled data from Alabama and Mississippi, which had similar distributions and small sample sizes. The results of significant "global" tests elicited a subsequent round of component tests that examined paired comparisons within the Gulf and southeast Atlantic regions, and within Florida. All tests were two-tailed, and α was set at $P < 0.05$. We conducted all analyses using SPSS ver. 13 (SPSS Inc. 2005).

RESULTS

Wintering distributions were based on a subset of 661 specimens (Table 1) of a total of 978 non-breeding specimens we examined from the Atlantic and Gulf coasts (Appendix 2). Saltmarsh Sparrows constituted 37% and Nelson's Sparrows 63% of the sample (Table 1). We identified three specimens that we regarded as hybrids between *A. c. caudacutus* × *A. n. subvirgatus* (one each in North Carolina, South Carolina, and Florida).

Wintering Distributions of Species.—Saltmarsh and Nelson's sparrows winter in maritime localities from North Carolina south along the Atlantic coast and west along the Gulf coast (Fig. 1). Among Saltmarsh Sparrows examined ($n = 245$), only 7% (18) were from sites in Virginia, Maryland or New York (Table 1). The westernmost locality was Wakulla County, Florida, on the Gulf coast (Fig. 1). Most specimens were collected on the Atlantic coast from North Carolina to northeast Florida. Secondary concentrations of specimens were in south Florida ($n = 17$) (Table 1, Fig. 1), primarily in the Cape Sable area (Everglades National Park), and on the west-central Gulf coast of Florida (61 specimens, most [$n = 47$] occurring in just two counties, Pinellas and Pasco) (Table 1, Fig. 1).

Nelson's Sparrows wintered widely from New England to Texas along the coast. Their core range in winter occurred from North Carolina south to Florida and west to Texas. However, few were taken in south Florida (6 of 23 specimens, Table 1). Of these ($n = 13$), only one occurred in extreme southwest Florida in the Cape Sable area. West of Wakulla County, Florida, only Nelson's Sparrows were present. Our westernmost records were in Neuces County, Texas (Fig. 1).

The wintering ranges of the two species of sparrows overlapped completely from New York south along the Atlantic coast. Saltmarsh Sparrows occurred more frequently than Nelson's Sparrows from North Carolina north in winter (Table 1). About two-thirds (66%) of all the wintering sharp-tailed sparrows in North Carolina were Saltmarsh Sparrows. Nelson's Sparrows predominated from South Carolina to northeast Florida (Table 1). The relative occurrence of the two species in North Carolina differed significantly from their representation in South Carolina (80% Nelson's Sparrows; $\mathrm{X}^2 = 29.3$, df = 1, $P < 0.001$). The North Carolina distribution also differed from that in Georgia (52% Nelson's Sparrows; $\mathrm{X}^2 = 6.1$, df = 1, $P < 0.013$), and in northeast Florida (68% Nelson's Sparrows; $\mathrm{X}^2 = 15.4$,

TABLE 1. Number (percent) of Saltmarsh (*Ammodramus caudacutus*) and Nelson's (*A. nelsoni*) sparrow specimens taken as wintering[a] birds along the Atlantic and Gulf coasts of the United States. Species- and subspecies-rank identifications are compiled separately in different panels, and summarized by state and region. Percentages are comparisons among states and in the Gulf region.

	Species[b]			Saltmarsh Sparrow subspecies[c]		Nelson's Sparrow subspecies[c]		
Region	Total records	*A. caudacutus*	*A. nelsoni*	*A. c. caudacutus*	*A. c. diversus*	*A. n. nelsoni*	*A. n. alterus*	*A. n. subvirgatus*
Massachusetts	5	0 (0)	5 (1.2)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.5)
New York	3	2 (0.8)	1 (0.2)	1 (1.2)	0 (0)	0 (0)	0 (0)	0 (0)
Maryland	8	8 (3.2)	0 (0)	3 (3.5)	4 (3.2)	0 (0)	0 (0)	0 (0)
Virginia	9	8 (3.2)	1 (0.2)	5 (5.9)	1 (0.8)	0 (0)	0 (0)	0 (0)
North Carolina	74	49 (20.0)	25 (6.0)	18 (21.2)	24 (19.0)	16 (7.3)	3 (5.4)	0 (0)
South Carolina	56	11 (4.5)	45 (10.8)	4 (4.7)	5 (4.0)	6 (2.7)	9 (16.4)	22 (32.4)
Georgia	105	50 (20.3)	55 (13.3)	13 (15.3)	32 (25.4)	20 (9.1)	13 (23.6)	7 (10.3)
Florida	288	118 (48.0)	170 (41.0)	41 (48.2)	60 (47.6)	82 (37.4)	24 (43.6)	38 (55.9)
Northeast	127	40	87	15	18	26	15	36
South	23	17	6	4	11	4	0	0
Northwest	115	61	54	22	31	44	4	0
Panhandle	23	0	23	0	0	13	4	0
Alabama	9	0 (0)	9 (2.2)	0 (0)	0 (0)	7 (3.2)	2 (3.6)	0 (0)
Mississippi	13	0 (0)	13 (3.1)	0 (0)	0 (0)	12 (5.5)	1 (1.8)	0 (0)
Louisiana	61	0 (0)	61 (14.7)	0 (0)	0 (0)	51 (23.3)	3 (5.4)	0 (0)
Texas	30	0 (0)	30 (7.2)	0 (0)	0 (0)	25 (11.4)	0 (0)	0 (0)
Gulf[d]	136	0 (0)	136 (32.8)	0 (0)	0 (0)	106 (48.4)	10 (18.2)	0 (0)
Totals	661	246	415	85	126	219	55	68

[a] For Atlantic states south to Georgia, "wintering" records are specimens taken December through March (winter season); for Florida and the Gulf states, all specimens are wintering records.

[b] All specimens were assignable to species, with no identification conflicts.

[c] Only specimen records of conforming identifications between JSG and GEW are shown. The difference between the total number of subspecies records within a state or region and the value in "Total records" is the number of censored specimen records (intergrades, identification conflicts).

[d] "Gulf" region comprises the Florida Panhandle subregion and all northern Gulf states, Alabama to Texas. The percentage here is the relative proportion of total species or subspecies specimen records represented in the region.

df = 1, $P < 0.001$). The number of specimens of wintering sharp-tailed sparrows from Maryland and Virginia was small, but Saltmarsh Sparrows were more likely there (94%) than Nelson's Sparrows (Table 1). All winter specimens of sharp-tailed sparrows from Massachusetts ($n = 5$) were Nelson's Sparrows, and constituted the northernmost winter records of this species in our study (Table 1).

Winter Distributions of Subspecies.—Core wintering distributions of all subspecies were within the coastal region between North Carolina and Texas (Figs. 2, 3). Among all specimens that we diagnosed, we found only 15 winter records of identified subspecies from Virginia north (Table 1). We rejected the null hypothesis that subspecies occurrences from North Carolina to Texas were independent samples from a single, homogenous, wintering community of sharp-tailed sparrows ($X^2 = 262.86$, df = 24, $P = 0.000$).

The most northern record of *A. c. caudacutus* was in New York, and for *A. c. diversus* in Maryland. The wintering distributions of these two subspecies were coincident from North Carolina to Florida. Most western records for both subspecies were in Wakulla County, Florida, on the Gulf coast (Fig. 2). Occurrence frequencies of the two subspecies among states were similar ($X^2 = 2.48$, df = 3, $P = 0.48$) (Table 1).

A. n. nelsoni from the northern Great Plains occupied the most extensive wintering range among the five subspecies of sharp-tailed sparrows (Table 1; Figs. 2, 3). It mainly occurred in winter from North Carolina south and west to Texas (Fig. 3). *A. n. alterus*, representing breeding birds from the interior bays, wintered primarily on the Atlantic coast from North Carolina to northeast Florida, and in smaller numbers on the Gulf coast. The relative occurrence of this subspecies west of the Florida panhandle diminished across Alabama and Mississippi (13.6%, pooled) to Louisiana (5.6%) (Fig. 3). The northernmost winter records were in North Carolina ($n = 2$, Fig. 3).

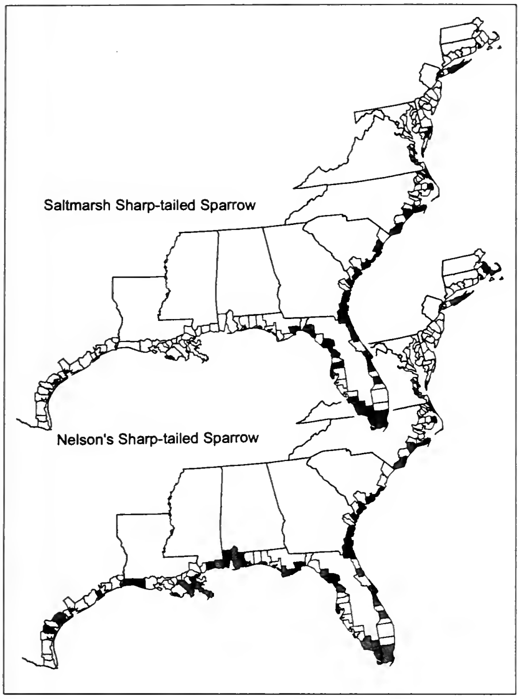

FIG. 1. Wintering distributions of Saltmarsh and Nelson's Sharp-tailed sparrows in the eastern United States by county or parish (Louisiana) based on specimen occurrences. Shading indicates sample size range: 1–4 (gray), ≥5 (black; maximum n = 177).

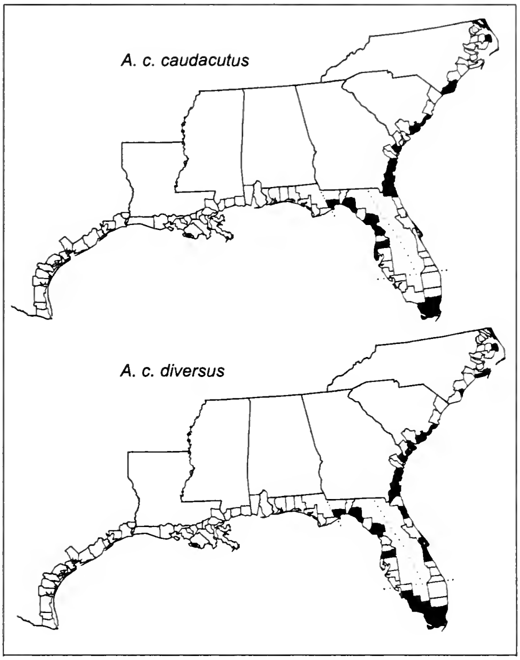

FIG. 2. Core wintering distributions of subspecies of Saltmarsh Sharp-tailed Sparrow by county. Shading indicates sample size range: 1–4 (gray), ≥5 (black; maximum n = 37).

A. n. subvirgatus, the northeastern Atlantic breeding birds, occupied the narrowest wintering range among the subspecies from South Carolina to northeastern Florida. Northern outliers were in Massachusetts (n = 1) and North Carolina (n = 1), and the most southern record was along the central Atlantic coast of Florida (n = 1, Fig. 3). This subspecies was unrecorded on the Gulf coast.

The composition of sharp-tailed sparrows within each of the four subregions of Florida was notably distinct (X^2 = 114.40, df = 12, P = 0.000; Fig. 4). The northeastern subregion is the only part of Florida in which all subspecies of both species winter (Figs. 2, 3). The wintering sharp-tailed sparrow population in south Florida, most strongly represented by subspecies of *A. caudacutus*, is isolated from birds in the northeast and northwest subregions, and currently is relatively small. The composition of the wintering sparrow population in the panhandle is the most divergent. This population is predominately represented by *A. n. nelsoni*, and conforms to the same pattern present in Alabama, Mississippi, and Louisiana (Table 1).

Migration in Sharp-tailed Sparrows.—We examined 465 specimens of both species, including 27 specimens from interior and subcoastal locations, obtained in fall and spring migration periods. We restricted our analysis of migratory patterns along the Atlantic coast to specimens taken in states north of Florida during these periods.

Saltmarsh Sparrows (n = 201) during migration were confined to coastal locations from Massachusetts to Georgia. Nelson's Sparrows (n = 237) occurred along the Atlantic coast and far inland. Most of the inland records were passage migrants either approaching or leaving the Gulf coast. We confirmed the occurrence of this species during migration at four subcoastal localities up to 80 km inland (n = 10; North Carolina, Florida, Louisiana), and at interior, continental localities in Georgia (n = 3), Tennessee (n = 4), and Kansas (n = 5).

Occurrences (shaded counties) and inferred

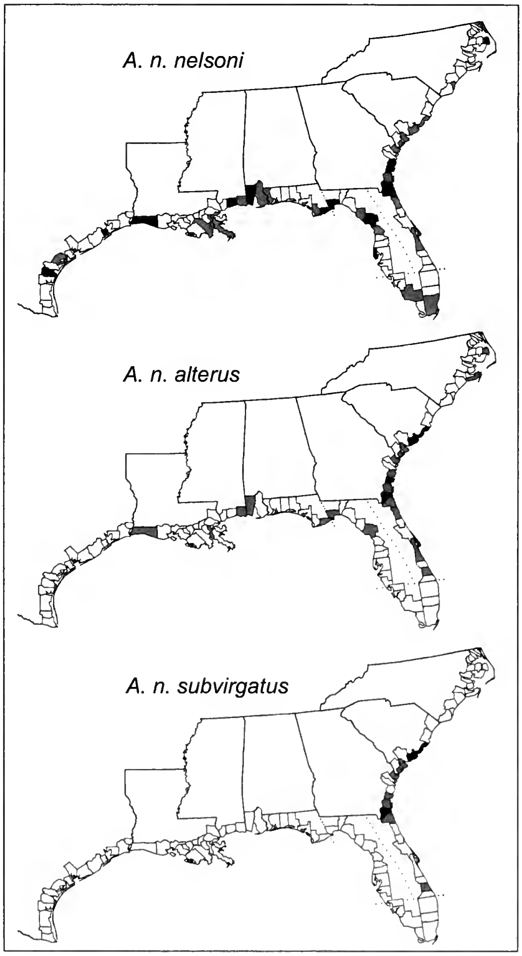

FIG. 3. Core wintering distributions of subspecies of Nelson's Sharp-tailed Sparrow by county. Shading indicates sample size range: 1–4 (gray), ≥5 (black; maximum *n* = 55).

migratory routes (arrows) of *A. n. nelsoni* during migration in central and eastern United States varied geographically (Fig. 5). This subspecies occurs in fall migration along the Atlantic coast from Massachusetts south and throughout the Mississippi River watershed from eastern South Dakota to eastern Texas, and east to the Appalachian Mountains. Distribution of occurrences during spring migration is similar to that during fall migration in the interior of the continent. We documented this subspecies along the Atlantic coast in spring only as far north as Virginia (*n* = 2) and Maryland (*n* = 1).

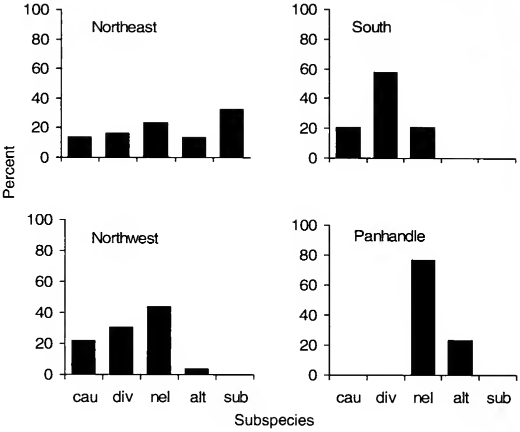

FIG. 4. Occurrence (%) of subspecies of Saltmarsh and Nelson's Sharp-tailed sparrows within each subregion (northeast, south, northwest, panhandle) of Florida. Abbreviations are: cau, *A. c. caudacutus*; div, *A. c. diversus*; nel, *A. n. nelsoni*; alt, *A. n. alterus*; sub, *A. n. subvirgatus*.

Most *A. n. alterus* occurred along the Atlantic coast during migration. However, we examined three specimens that were "typical" *alterus* from deep inland or in southern, subcoastal locations. One of these (LSU 77292) was killed at a television tower near Nashville, Tennessee (Davidson County) on 25 September 1955. Another was taken in Athens, Georgia (Clarke County) on 19 October 1925 (USNM 339818). The third was obtained in Bladen County, North Carolina, on 18 October 1971 (UNCW B308). These records represent the first evidence that some northern bay breeders may follow inland routes in the fall south of the northeastern United States. The extremes of migration dates in Saltmarsh Sparrows were 2 October and 17 May, and in Nelson's Sparrows were 24 September and 28 May (Table 2).

DISCUSSION

Dataset Bias and Sources of Error.—Identification agreement between us varied from 88 to 99%, depending on subspecies. We previously recognized likely identification biases in the diagnostic key that we developed. Our concepts of plumage variation in *A. c. caudacutus* and *A. n. alterus* were conservative relative to *A. c. diversus* and *A. n. nelsoni*, respectively. This meant that darker specimens of *A. c. caudacutus* were likely to be classified as *A. n. diversus*, and that bright,

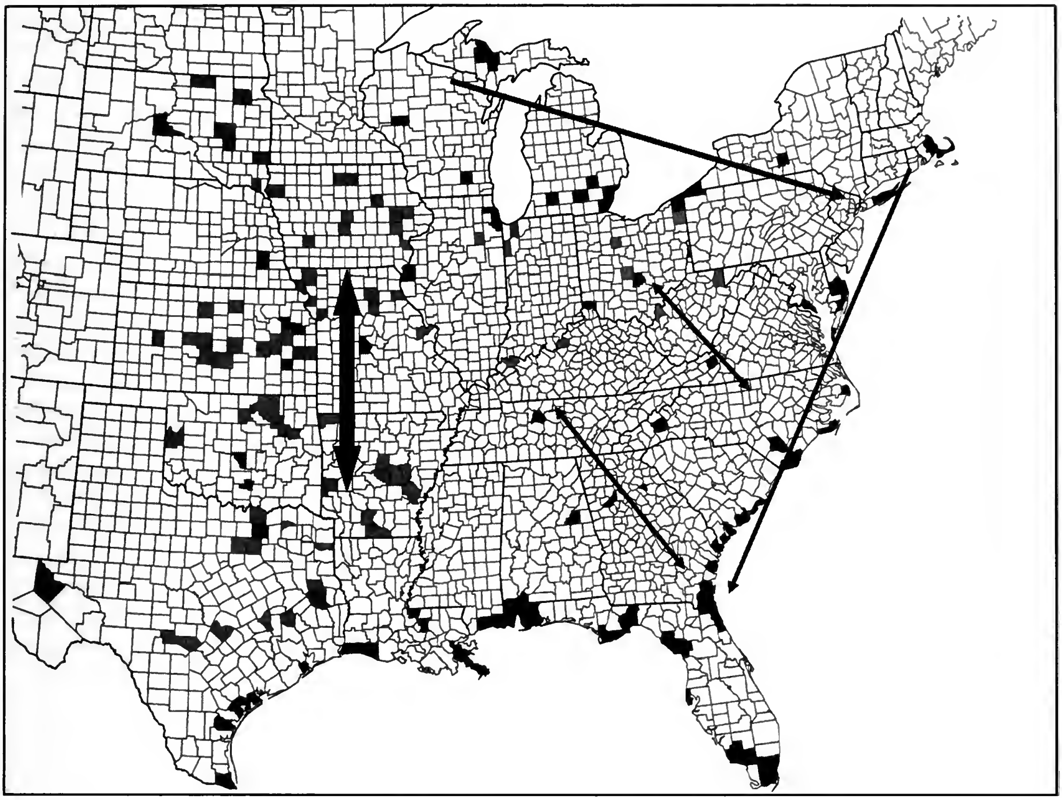

FIG. 5. Occurrences of *A. n. nelsoni* in the eastern United States during spring and fall migrations based on specimens seen by us or by others (counties shaded black), and on observation reports from the literature presumed to be this subspecies (counties shaded gray). Arrows indicate inferred migration routes. Citations used to compile this map are in the DISCUSSION.

strongly marked variants of *A. n. alterus* were likely to be assigned to *A. n. nelsoni*. We must consider how these biases may have impacted our understanding of winter distributions.

Often such unusual cases resulted in identification conflicts between us, and were censored from our analysis. Thus, the double-identification methodology applied here partly mitigated a tendency to misdiagnose extreme variants of *A. c. caudacutus* and *A. n. alterus*.

TABLE 2. Earliest arrival and latest departure dates of subspecies of Saltmarsh and Nelson's Sharp-tailed sparrows on their wintering grounds.

	Saltmarsh Sharp-tailed Sparrow		Nelson's Sharp-tailed Sparrow					
	A. c. caudacutus/diversus		*A. n. nelsoni*		*A. n. alterus*		*A. n. subvirgatus*	
Region	Arrival	Departure	Arrival	Departure	Arrival	Departure	Arrival	Departure
North Carolina	—	—	27 Sep	18 May	24 Sep	27 May	—	—
South Carolina	02 Oct	17 May	01 May	25 May	04 Oct	28 May	14 Oct	29 May
Georgia	10 Oct	27 Apr	20 Oct	27 May	19 Oct	10 May	—	11 Apr
Florida[a]	06 Oct	11 Apr	01 Oct	14 May	02 Oct	13 May	16 Oct	25 Mar
Gulf[b]	—	—	21 Sep	23 May	17 Oct	—	—	—

[a] Peninsular Florida west to Wakulla County.

[b] Northern Gulf coast from Florida panhandle (Franklin County) west to Texas.

Still, the identification bias in Saltmarsh Sparrows may have resulted in a failure to detect a difference between the relatively restricted ranges of the two subspecies involved. In contrast, it is unlikely that identification bias in Nelson's Sparrows compromised our ability to characterize the widespread distributions of these two subspecies. The relatively large differences between the core wintering ranges of the subspecies of Nelson's Sparrows makes geographic sense. Also, our delineation of the westward limit of the wintering distribution of *A. n. alterus* erred, if anything, on the conservative side.

We are aware of the potential limitations that arise from use of specimen data. Specimen samples are typically non-random in relation to years or localities they represent. In our case, nearly 75% of the specimens that we examined were collected before 1950. We estimate, however, that we probably saw ~80% of the non-breeding sharp-tailed sparrow specimens in collections taken along the Atlantic and Gulf coasts south of Maryland. Also, the core wintering ranges of the five subspecies based on post-1950 data were similar to those documented by our pre-1950 sample. In our discussion of wintering distributions, we use recent published information to evaluate patterns of wintering based heavily on old specimens.

Wintering Distributions.—This is the first specimen-based study of wintering distributions of the subspecies in the sharp-tailed sparrow complex (but see Montagna 1942). Important published summaries of the wintering ranges of the five subspecies treated here are AOU (1957) and Paynter (1970). Hill's (1968) review is a restatement of what appeared in AOU (1957), which was the last *AOU Check-list* to cover distributions of subspecies. More recently published information pertaining to winter occurrences is in state or regional avifaunal treatments (e.g., Bull 1964, 1974; Oberholser 1974; Veit and Petersen 1993; Stevenson and Anderson 1994).

Some previous specimen misidentifications have been accepted in older literature, and have resulted in erroneous statements on the western extent of wintering in *A. c. diversus* (AOU 1957, 1998) and *A. n. alterus* (Oberholser 1974) along the Gulf coast. *A. c. diversus* was listed as far west as Louisiana (AOU 1957) and casually to coastal Texas (AOU 1998). *A. n. alterus* was reported from Texas as well. These assessments evidently were based on specimens misidentified by Oberholser (1938; *diversus* in Louisiana) and Oberholser (1974). We re-examined most of the specimens involved, and two other specimens misidentified as *A. n. alterus* from Texas (Oberholser 1974), and considered them to represent either *A. n. nelsoni* or an intergrade (one case) between *A. n. nelsoni* and *A. n. alterus*. Thus, we found *A. c. diversus* only as far west as Wakulla County, Florida, and casual occurrence of *A. n. alterus* to Cameron Parish, Louisiana. A recent observational report of a Saltmarsh Sparrow in Santa Rosa County, Florida, suggests vagrancy to the western panhandle (Pranty 2002).

We were surprised to learn that two relatively small, currently highly disjunct populations of Saltmarsh Sparrows occur in Everglades National Park (Monroe County) and in west-central Florida on the Gulf coast (Figs. 1, 2). Saltmarsh Sparrows predominated in our samples in Pinellas and Pasco counties, with diminishing relative occurrence north to Wakulla County. We suggest these relatively isolated wintering populations resulted from restriction and loss of once more prevalent coastal marshes where Saltmarsh Sparrows commonly wintered in south Florida north to the central-west Gulf coast during the Pleistocene and early Holocene. Mangroves (e.g., *Rhizophora mangle*) became more prevalent in south Florida during the Holocene, advanced north along the coasts, and displaced most of the southernmost *Spartina* marshes that may have occurred on the broad, exposed Pleistocene platform (Webb 1990). Urbanization has further restricted coastal wetlands, including salt marshes, in south Florida. We hypothesize that site tenacity promoted continued occupation of historic wintering grounds in south Florida as long as remnant marshes persisted.

Specimen-based winter records are sparse along the northeastern Atlantic coast. We know that some individuals may overwinter during mild seasons as far north as New York (Elliott 1962, Post 1970) and Nova Scotia (McLaren 1994, 2002). However, some may succumb to freezing temperatures or withdraw as winter progresses (Grant and Kirby-Smith 1992).

Saltmarsh Sparrows continue to occur in the two disjunct Gulf coast populations identified by our specimen samples on the Florida peninsula (Post 1998; Pranty 1998a, 1998b, 2004). Recent observations suggest that Nelson's Sparrows also occur in Everglades National Park in winter (Pranty 2001, 2002).

Migration Routes.—Autumnal and vernal migrations of Saltmarsh Sparrows apparently are restricted to a route along the Atlantic coast. Inland vagrancy and subcoastal inland encounters are noteworthy when they occur (Poole 1964, Parkes 1992).

A. n. subvirgatus also confines nearly all its migratory movements to the coast. The exceptions may be in Massachusetts and Connecticut. Inland specimens, which we have not seen, have been identified tentatively as *A. n. subvirgatus* from along the Connecticut River (Springfield, Massachusetts; Portland, Connecticut), and in eastern Massachusetts (Wayland) (Sage 1891, Griscom and Snyder 1955, Veit and Petersen 1993). These occurrences may indicate a tendency for some individuals to move directly across southeastern New England to the Connecticut and New York coasts bypassing the easterly landmass of the Cape Cod peninsula. Far inland reports from western New York (e.g., Burtch 1897, Montagna 1942) have been re-evaluated as *A. n. alterus* (Bull 1974).

The issue of migration routes used by birds from the inland prairie and bay populations, *A. n. nelsoni* and *A. n. alterus*, respectively, is more complex. *A. n. alterus* mainly travels to the Atlantic coast via southern Ontario (inferred) and central New York (regular at Ithaca, Tompkins County; Bull 1974). We are not aware of any interior New England records of this subspecies during migration. The most western inland records of *A. n. alterus* are one specimen from Michigan (Livingston County, confirmed by W. E. C. Todd; Mumford and Zimmerman 1958), one from Ohio (Lake County; Peters 1942), and eight from Pennsylvania (Erie County, identified by K. C. Parkes [1992]). We add records from Tennessee (Davidson County) and inland Georgia (Clarke County). These records suggest the possibility that some *A. n. alterus* may reach the Gulf coast via direct inland routes.

A. n. nelsoni is widely understood to migrate along the Atlantic coast and through the eastern interior of the United States (Fig. 5, based on Trautman 1940, Wood 1951, Graber 1953, Tordoff and Mengel 1956, Mumford and Zimmerman 1958, Poole 1964, Mengel 1965, Sutton 1967, Lowery 1974, Oberholser 1974, Imhof 1976, Faanes 1981, Hall 1983, Dinsmore et al. 1984, Mlodinow 1984, Bray et al. 1986, Brock 1986, James and Neal 1986, Monroe et al. 1988, Peterjohn 1989, Robbins 1991, South Dakota Ornithologists' Union 1991, Robbins and Easterla 1992, Thompson and Ely 1992, Monroe 1994, White 1999). Evidently relatively few birds move east to the New England coast of Massachusetts in the fall (Veit and Petersen 1993). Transient *A. n. nelsoni* also frequently occur inland at Ithaca, New York in the fall (Bull 1974). In contrast, during spring migration, few or no birds of this race occur on the coast north of Virginia or Maryland (Bull 1964, Veit and Petersen 1993). We infer that birds of this subspecies wintering along the southeast Atlantic coast travel north in spring across inland Georgia (circum-montane route), and across the mountains (trans-montane route) from coastal North Carolina and South Carolina (Fig. 5). Reports from West Virginia also may represent trans-montane travel. We hypothesize the Atlantic coastal route is used in autumn, but perhaps not at all in spring. Significant movements southward in fall and northward in spring occur along a broad front through the Mississippi River watershed region directly to or from the Gulf coast.

CONSERVATION IMPLICATIONS

The breeding and wintering ranges of sharp-tailed sparrows occur in two of the most vulnerable and decimated habitat-types of North America, freshwater and maritime marshlands. The world distribution of Saltmarsh Sparrows is entirely within the United States, and that of Nelson's Sparrows is wholly in Canada and the United States. The entire wintering range of both species is in the United States. All Saltmarsh Sparrow populations, and nearly all interior bay and Canadian Atlantic populations of Nelson's Sparrows, occupy a narrow, highly fragmented fringe of coastal wetlands, much of which has been modified by drainage ditching (United States) and agricultural diking (Maritimes) (Dahl 1990, Greenlaw and Rising 1994).

Sharp-tailed sparrows are probably most vulnerable on their wintering grounds as broadly distributed breeding populations are concentrated in a thin and fragmented fringe of coastal wetlands in winter. *A. n. subvirgatus* has the most restricted wintering range of all sharp-tailed sparrow subspecies, from South Carolina to extreme northeastern Florida. The global population of this subspecies is dependent on the health and integrity of the salt marshes in this small area. Wetland policy in the United States alone can have a major impact on the welfare of all sharp-tailed sparrows.

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APPENDIX 1.

Diagnostic key to the species and subspecies of sharp-tailed sparrows in the genus *Ammodramus*.

Note in Explanation.—This key is based on breeding specimens. Sample sizes for each taxon are listed with bill measurements (mm, nares to tip: mean ± SD). Comparisons reflect typical (widespread) expressions of pattern and hue among different populations. The first couplet (A, AA) distinguishes the species *Ammodramus caudacutus* from *A. nelsoni*. Capitalized color names (e.g., Clay [chip 123B]) are from Smithe (1975). In subjective assessments of specimens to racial groups, we recognize that *A. c. caudacutus* and *A. n. nelsoni* are especially variable in some plumage characters, and that differentiation of *A. c. caudacutus* versus *A. c. diversus* and *A. n. nelsoni* versus *A. n. alterus* is particularly problematic. As a conservative practice, an investigator should accept only clear-cut examples of *A. c. diversus* or *A. n. alterus* in making racial assignments. Defaults in difficult choices are intergrades. **Bolding** facilitates comparisons between couplets.

A. **Malar** region (orange ocher or orange Clay) and **breast** (Yellow Ocher or pale Clay) strongly contrasting; **inner tertials** (T2, T3) with conspicuous submarginal black bars framing inner edge of pale fringe apically; **breast** with distinct blackish stripes centrally; **bill** longer; (**9.3 mm ± 0.32** [*n* = 92]) . . . . *A. caudacutus* subspp.

  B. **Dorsum** background color Raw Umber without strong dusky tone (browner); **crown** with black streaks more or less restricted to lateral stripes, and olive-grayish median stripe usually distinctly demarcated from brown lateral stripes; **tertials** with black submarginal stripe strongly contrasting with olive brown center; **dorsum pattern** weakly contrasty (scapular centers Raw Umber), with black restricted as submarginal bar bordering dingy white or grayish fringe; (**9.3 ± 0.30** [*n* = 67]) . . . . *A. c. caudacutus*

  BB. **Dorsum background** color Raw Umber with strong dusky tone (blackish); **crown** strongly streaked with black, reducing contrast between lateral and median stripes; **tertials** with black submarginal stripe weakly contrasting with blackish center, or obscured; **dorsum pattern** strongly contrasty (scapular centers black), with black broadly bordering buffy white fringe; (**9.2 ± 0.34** [*n* = 25]) . . . *A. c. diversus*

AA. **Malar** region (Yellow Ocher or bright yellow Clay) and **breast** (yellow Clay) with little (sometimes moderate) or no contrast; **inner tertials** with uniform dark centers (black, brownish black), lacking distinct submarginal bar apically along inner fringe edge; **breast** typically with indistinct, blurred streaks, or with little or no streaking centrally (some *A. n. nelsoni* have dark mid-breast streaks as in A., but this is infrequent); **bill** shorter; (**8.4 mm ± 0.27** [*n* = 148]) . . . . . *A. nelsoni* subspp.

  B. **Flanks** with streaking distinct, dark; **dorsum** moderately to strongly patterned, typically with extensive development of black centers in scapulars, strongly contrasting with white or buffy fringes; **auricular** patch weakly differentiated, suffused with Clay or ocher; **crown** strongly patterned with heavy black streaking in lateral stripes, and olive-gray median stripe reduced (narrowed) or obscured by black. (**8.3 ± 0.26** [*n* = 41]) . . . . *A. n. nelsoni*

  BB. **Flanks** with streaking indistinct, blurred, grayish; **dorsum** weakly patterned, with little to moderate development of black, and clear gray to dull cream fringes; **auricular** patch more discrete, grayish; **crown** with black streaking reduced in lateral stripes, and with broader, more obvious clear gray or olive gray median stripe.

C. **Dorsum** background color bright Raw Umber (warm bronzy tone, as in *A. n. nelsoni*), more strongly contrasting with gray or whitish scapular edges; **face triangle** and **breast** bright Clay or ocher (similar to *A. n. nelsoni*); **crown** with median stripe bluish gray, often relatively broad, and with black streaks in lateral stripes evident; **edging on secondary coverts** often moderately to strongly rufescent (greater coverts, T1); (**8.3 ± 0.26** [*n* = 28]) . . . . . . *A. n. alterus*

CC. **Dorsum** background color dull, with strong olive-grayish tone, little development of black, weakly contrasting with pale scapular edges; **face triangle** and **breast** dull (yellowish) Clay or ocher; **crown** with median stripe dull olive-gray, not strongly contrasted with brown lateral stripes, and with black streaks in laterals absent or nearly so; **edging on secondary coverts** weakly rufescent, or cinnamon; (**8.6 ± 0.28** [*n* = 79]) . . . .*A. n. subvirgatus*

APPENDIX 2. Number (percent) of all non-breeding, coastal specimens of sharp-tailed sparrows examined in this study compiled by state and county or parish. Percentages represent comparisons among states (column subtotal/column grand total × 100). Abbreviations are cau = *A. c. caudacutus*, div = *A. c. diversus*, sub = *A. n. subvirgatus*, alt = *A. n. alterus*, and nel = *A. n. nelsoni*.

State	County	Total records	Total cau[a]	Total nel[a]	Saltmarsh Sparrow[b]		
					cau	cau/div	div
Massachusetts[c]							
	Plymouth	2	0	2	0	0	0
	Barnstable	3	0	3	0	0	0
	Subtotals	5 (0.5)	0 (0)	5 (0.8)	0 (0)	0 (0)	0 (0)
New York[c]							
	Suffolk	3	2	1	2	0	0
	Subtotals	3 (0.3)	2 (0.6)	1 (0.2)	2 (1.6)	0 (0)	0 (0)
Maryland[c]							
	Worcester	8	8	0	3	0	4
	Subtotals	8 (0.8)	8 (2.2)	0 (0)	3 (2.4)	0 (0)	4 (2.2)
Virginia[c]							
	Northampton	9	8	1	5	0	1
	Subtotals	9 (0.9)	8 (2.2)	1 (0.2)	5 (4.1)	0 (0)	1 (0.5)
North Carolina							
	Currituck	5	2	3	0	0	1
	Pasquotank	2	2	0	1	0	1
	Dare	67	43	24	15	3	23
	Craven	1	1	0	0	0	1
	Carteret	25	18	7	4	2	9
	Onslow	7	6	1	3	0	3
	New Hanover	13	4	8	3	0	1
	Bladen	2	1	1	0	0	0
	Brunswick	5	1	4	1	0	0
	Unlocalized	4	1	3	0	0	1
	Subtotals	131 (13.4)	79 (22.0)	51 (8.3)	27 (22.1)	5 (33.3)	40 (21.5)
South Carolina							
	Georgetown	1	1	0	0	0	1
	Charleston	247	69	177	24	3	37
	Beaufort	33	6	27	0	0	6
	Unlocalized	1	1	0	0	0	0
	Subtotals	282 (28.8)	77 (21.4)	204 (33.2)	24 (19.7)	3 (20.0)	44 (23.6)
Georgia							
	Chatham	29	12	17	6	1	2
	McIntosh	33	19	14	2	0	15
	Glynn	50	22	28	6	0	14
	Camden	28	14	14	6	1	6
	Subtotals	140 (14.3)	67 (18.7)	73 (11.9)	20 (16.4)	2 (13.3)	37 (19.9)
Florida							
	Nassau	98	30	68	14	1	14
	Duval	12	2	10	1	0	0
	St. Johns	5	2	3	0	0	1
	Flagler	1	1	0	0	1	0
	Brevard	8	4	4	0	0	3
	St. Lucie	3	1	2	0	0	0
	Miami-Dade	4	2	2	1	0	1
	Monroe	14	13	1	3	0	8
	Collier	4	1	3	0	0	1
	Lee	1	1	0	0	0	1
	Pinellas	49	39	9	14	2	19
	Pasco	8	8	0	2	1	4
	Citrus	2	1	1	1	0	0
	Levy	29	7	22	2	0	5

APPENDIX 2. Extended.

	Nelson's Sparrow[b]				
Hybrid	sub	sub/alt	alt	alt/nel	nel
0	1	0	0	1	0
0	0	0	0	3	0
0 (0)	1 (1.1)	0 (0)	0 (0)	4 (5.8)	0 (0)
0	0	0	0	1	0
0 (0)	0 (0)	0 (0)	0 (0)	1 (1.9)	0 (0)
0	0	0	0	0	0
0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
0	0	0	0	0	0
0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
0	0	0	0	0	3
0	0	0	0	0	0
0	0	0	2	4	16
0	0	0	0	0	0
0	0	0	3	0	4
0	0	0	1	0	0
1	1	0	3	0	3
0	0	0	1	0	1
0	0	0	1	0	2
0	0	0	0	1	2
1 (33.3)	1 (1.1)	0 (0)	11 (9.4)	5 (9.6)	31 (10.4)
0	0	0	0	0	0
1	36	3	55	19	47
0	6	0	3	1	16
0	0	0	0	0	0
1 (33.3)	42 (46.2)	3 (75.0)	58 (49.6)	20 (38.5)	63(21.2)
0	4	0	6	1	5
0	0	1	1	3	8
0	2	0	9	3	8
0	3	0	2	1	5
0 (0)	9 (9.9)	1 (0.25)	18 (15.4)	8 (15.4)	26 (8.8)
0	33	0	11	5	15
0	2	0	1	0	6
0	0	0	1	0	2
0	0	0	0	0	0
0	0	0	1	0	3
0	1	0	1	0	0
0	0	0	0	1	1
0	0	0	0	0	0
0	0	0	0	0	3
0	0	0	0	0	0
1	0	0	0	0	8
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	2	2	16

APPENDIX 2. Continued.

					Saltmarsh Sparrow[b]		
State	County	Total records	Total cau[a]	Total nel[a]	cau	cau/div	div
	Dixie	2	0	2	0	0	0
	Taylor	2	2	0	1	0	1
	Wakulla	20	4	16	2	0	2
	Franklin	16	0	16	0	0	0
	Gulf	1	0	1	0	0	0
	Escambia	6	0	6	0	0	0
	Unlocalized	2	0	2	0	0	0
	Subtotals	287 (29.3)	118 (32.8)	168 (27.3)	41 (33.6)	5 (33.3)	60 (32.2)
Alabama							
	Baldwin	1	0	1	0	0	0
	Mobile	8	0	8	0	0	0
	Subtotals	9 (0.9)	0 (0)	9 (1.5)	0 (0)	0 (0)	0 (0)
Mississippi							
	Jackson	4	0	4	0	0	0
	Harrison	9	0	9	0	0	0
	Subtotals	13 (1.3)	0 (0)	13 (2.1)	0 (0)	0 (0)	0 (0)
Louisiana							
	E Baton Rouge	2	0	2	0	0	0
	Plaquemines	4	0	4	0	0	0
	Orleans	4	0	4	0	0	0
	Jefferson	5	0	5	0	0	0
	Lafourche	2	0	2	0	0	0
	Cameron	44	0	44	0	0	0
	Subtotals	61 (6.2)	0 (0)	61 (9.9)	0 (0)	0 (0)	0 (0)
Texas							
	Galveston	10	0	10	0	0	0
	Aransas	1	0	1	0	0	0
	Refugio	1	0	1	0	0	0
	Neuces	18	0	18	0	0	0
	Subtotals	30 (3.1)	0 (0)	30 (4.9)	0 (0)	0 (0)	0 (0)
Grand Totals		978	359	616	122	15	186

[a] Totals in these columns include all specimens assignable to species, including those involving identification conflicts between JSG and GEW at the subspecies rank. The value in "Total Records" is the sum of "Total cau" and "Total nel."

[b] Totals in these columns represent all conforming identifications between JSG and GEW at the subspecies rank or in categories of intergrades (e.g., cau/div).

[c] Winter-season (Dec through Mar) specimens only were examined from these states. In other states, all non-breeding specimens (Sep to May) examined were tallied.

APPENDIX 2. Continued, Extended.

	Nelson's Sparrow^b				
Hybrid	sub	sub/alt	alt	alt/nel	nel
0	0	0	0	0	2
0	0	0	0	0	0
0	0	0	3	0	13
0	0	0	4	0	8
0	0	0	0	0	1
0	0	0	0	1	3
0	2	0	0	0	0
1 (33.3)	38 (41.8)	0 (0)	24 (20.5)	9 (17.3)	82 (27.6)
0	0	0	0	0	1
0	0	0	2	0	6
0 (0)	0 (0)	0 (0)	2 (1.7)	0 (0)	7 (2.4)
0	0	0	1	0	3
0	0	0	0	0	9
0 (0)	0 (0)	0 (0)	1 (0.8)	0 (0)	12 (4.0)
0	0	0	0	0	2
0	0	0	0	0	4
0	0	0	0	1	2
0	0	0	1	0	4
0	0	0	0	1	1
0	0	0	2	2	38
0 (0)	0 (0)	0 (0)	3 (2.6)	4 (7.7)	51 (17.2)
0	0	0	0	2	7
0	0	0	0	0	1
0	0	0	0	0	1
0	0	0	0	1	16
0 (0)	0 (0)	0 (0)	0 (0)	3 (3.8)	25 (8.4)
3	91	4	117	54	297

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PHILOPATRY AND NATAL DISPERSAL OF THE WESTERN SNOWY PLOVER

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ABSTRACT.—Conservation of threatened species requires knowledge of individual movements within and among spatially distinct subpopulations. We quantified philopatry, local dispersal, and number of breeding sites used by 62 Western Snowy Plovers (*Charadrius alexandrinus nivosus*) that were marked as chicks and returned to a breeding area in coastal northern California. Slightly more males (17%) than females (12%) returned to the study area. Natal dispersal (distance between natal nest and first nest as a yearling) was similar for males and females, and greater than reported for other shorebirds. Philopatric plovers dispersed shorter distances between successive nests within a breeding season compared to the distance between successive nests from one year to the next. Most males and females that bred locally wintered in the study area. Those that wintered locally tended to be from later clutches compared to the few migrants that hatched earlier in the season. The population of Snowy Plovers in coastal northern California is linked by dispersal with other breeding plovers along the Pacific coast. Dispersal estimates indicate that wide-ranging movements are typical of Snowy Plovers throughout their range, which should facilitate recolonization of habitats. *Received 17 March 2006. Accepted 4 September 2006.*

Conservation efforts for rare and patchily distributed species require knowledge of patterns and causes of dispersal of individuals among and within subpopulations. These data help biologists understand the genetic structure of populations (Avise and Hamrick 1996) and may enhance efforts to manage reproductive success. Dispersal estimates, as well as demographic data on survival and reproduction, are key elements of models predicting population persistence and recovery (Morris and Doak 2002). Dispersal is quantified in one of two ways (Oring and Lank 1984). First, philopatry is often gauged by the proportion of birds of either gender returning to breed at a location, although "return" at times is defined as an individual being observed (Colwell et al. 1988, Reynolds and Cooke 1988). This definition fails to distinguish between individuals seen once versus multiple times (resident) in an area. In contrast, natal dispersal quantifies the distance moved by a philopatric individual from its natal site to where it first breeds.

The Snowy Plover (*Charadrius alexandrinus*) in North America is divided into two subspecies (Page et al. 1995, Funk et al. 2007). One (*C. a. tenuirostris*) breeds in the Caribbean and a second (*C. a. nivosus*) is distributed in the western Great Plains, Great Basin, and along the Pacific coast. The U.S. Fish and Wildlife Service listed the Pacific coastal population segment in 1993 as threatened under the Endangered Species Act (U.S. Department of Interior 1993). The listed population segment has been well studied for over a quarter century (e.g., Warriner et al. 1986, Page et al. 1991). Stenzel et al. (1994, 2007) documented dispersal of a population in central California. Males and females occasionally dispersed long distances (50–1,140 km) within and between breeding seasons, and females were more likely than males to be absent from their primary site during a portion of the breeding season. Stenzel et al. (1994) interpreted these patterns as a consequence of the species' long breeding season (~120 days of egg laying), uniparental (male) care of chicks, and dynamic breeding habitats. These features allow females to nest successfully up to three times, often at widely disjunct locations.

The recovery plan for the listed population segment of the Western Snowy Plover (U.S.

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Department of Interior 2001) designated six recovery units extending from the northern limit of the species' breeding range in Washington south through California. Most breeding plovers in coastal northern California (Recovery Unit 2) are concentrated at a few locations around Humboldt Bay (Colwell et al. 2005b), which are several hundred km from other large concentrations of breeding plovers north and south. Recovery Unit 2 is targeted for a population of 150 breeding plovers (U.S. Department of Interior 2001), but the population has not reached this level, varying between 54 and 74 adults over a 6-year period (2001–2006; Mullin 2006).

We initiated a study in 2000 to individually mark breeding plovers in Recovery Unit 2. Our objectives were to examine gender differences in (1) return of plovers marked as chicks to the local breeding population, and (2) dispersal from natal nest to first and subsequent nests.

STUDY AREA

We studied plovers from 2000 to 2006 in Del Norte, Humboldt, and Mendocino counties in northern California (Fig. 1). We conducted most fieldwork in Humboldt County where the majority of plovers bred, but observers from state and federal agencies conducted bimonthly surveys of suitable breeding habitat throughout Recovery Unit 2. Plovers bred in two distinct habitats in the study area (Colwell et al. 2005b). Many plovers nested in fine, sandy substrates of ocean-fronting beaches amidst sparse debris fields of dried brown algae, shells, dead vegetation, driftwood, and occasional garbage. These beaches were often vegetated sparsely with native plants (e.g., *Abronia*, *Leymus*), dense stands of introduced European dune grass (*Ammophila arenaria*), and patches of sea rocket (*Cakile*). Plovers also nested on gravel bars of the lower Eel River near its confluence with the Pacific Ocean upriver approximately 16 km (Colwell et al. 2005b). Plovers breeding along the river nested in coarse, heterogeneous substrates varying in size from sand to pea-sized gravel and large stones, which were vegetated sparsely by willow (*Salix* spp.) and white sweet clover (*Melilotus alba*).

METHODS

We began marking adult plovers and newly hatched chicks in 2000, 1 year prior to initiating an intensive monitoring program. Each year, we captured breeding adults at nests using noose mats and circular walk-in nest traps. We marked adults with a unique combination of a federal aluminum band (wrapped in colored tape) and three colored leg bands. We marked all siblings of a brood at hatch with an aluminum band wrapped with brood-specific colored tape, which allowed us to distinguish between similar-age chicks from different broods in an area. We are confident that we captured and banded >95% of all newly hatched chicks and breeding adults in the study area each year. We recaptured adults that we first marked as chicks and marked them with unique adult band combinations. Observers surveyed breeding plovers almost daily in each habitat from mid March to early September. We recorded the identity of banded plovers, found nests, and monitored broods during surveys. Upon finding a nest, we recorded the number of eggs and estimated hatch date (for complete clutches) using egg flotation methods (Alberico 1995). We estimated hatch date for incomplete clutches by adding 27 days (average incubation period; Page et al. 1995) to the date the last egg was laid. We erected predator exclosures at most (61%) nests on beaches but did not construct exclosures around nests along rivers. We monitored fledging success of plovers beginning in 2001 through 2006 (Colwell et al. 2005a, 2007) by visiting sites with broods at 1–4 day intervals and recording the presence of adults and young until chicks fledged at 28 days (Page et al. 1995).

We defined philopatry as the breeding of a locally-hatched chick in the study area (coastal northern California; Recovery Unit 2 [RU2]) or repeated sightings during the nesting season suggesting breeding or attempted breeding. We quantified natal dispersal as the straight-line distance (m) between an individual's natal nest and its first nest as a yearling using a geographic information system. We categorized breeding dispersal, the distance between successive nests of an individual in two ways. Within-season dispersal was the distance between successive nests in a given

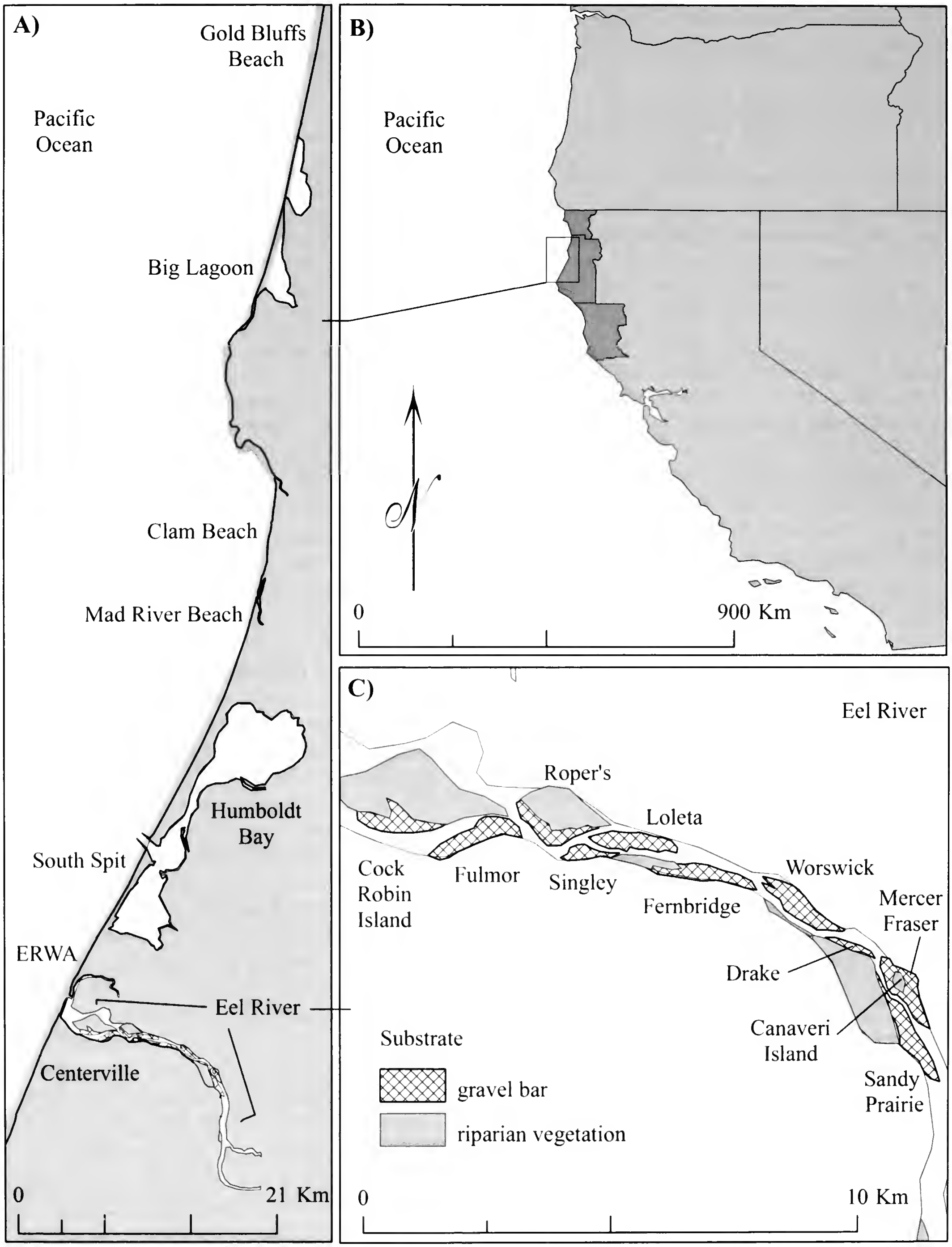

FIG. 1. Study areas (A) in the three counties of coastal northern California that comprise Recovery Unit 2; (B) where Snowy Plovers were color-marked and monitored from 2000 to 2006. Individual gravel bars along the lower Eel River are shown in (C).

TABLE 1. Philopatry of Snowy Plovers breeding in coastal northern California, 2001–2006.

Year	Total # banded previous year	% Return Females (n)[a]	% Return Males (n)[a]
2006	71	11 (4)	17 (6)
2005	76	11 (4)	16 (6)
2004	61	13 (4)	13 (6)
2003	69	14 (5)	12 (4)
2002	93	13 (6)	17 (8)
2001	58	7 (2)	24 (7)
Totals	428	11.7 (25)	17.3 (37)

[a] Assumes an equal sex ratio among newly hatched chicks (Székely et al. 2004).

breeding season; between-year dispersal was the distance between an individual's first nest of the year and the location of its last nest of the previous year. We summarized data for males and females separately, and distinguished between nests in which eggs failed to hatch and those in which at least one egg successfully hatched. We tallied the number of breeding locations occupied by individuals based on observations of color-marked birds. We defined a location (e.g., gravel bar or linear stretch of beach) as a breeding site occupied by one or more plovers, often separated by unsuitable (e.g., river channel, rocky intertidal) or unoccupied (e.g., long stretches of beach) habitat from other locations by a distance greater than the extent of any particular site (Fig. 1). We collated data over weekly intervals spanning 15 March to 15 July, the period in which plovers initiated nests (Colwell et al. 2005b) and prior to the formation of post-breeding flocks.

We analyzed return rates using Chi-square tests, assuming an equal sex ratio at hatch (Székely et al. 2004). Each individual plover was considered once in this analysis (i.e., returned either as a yearling or 2 years of age). We summarized dispersal as $\bar{x}$ ± SD, and compared samples for males and females using a t-test of untransformed linear distances between an individual's natal nest and first known nest as an adult. We used logistic regression to examine relationships between date of hatching for an individual and whether or not it was observed as a winter resident or migrant. We used SAS (SAS Institute 1991) to analyze data.

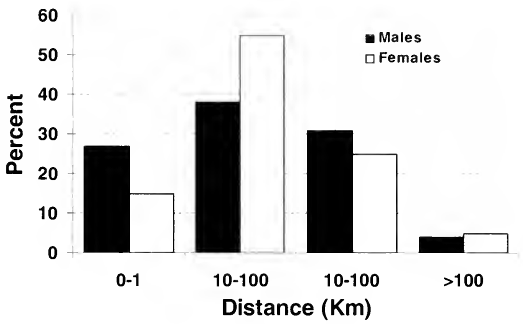

FIG. 2. Dispersal distances of Snowy Plovers (females [☐, n = 20] and males [■, n = 26]) in coastal northern California.

RESULTS

Philopatry and Natal Dispersal.—Sixty-two (14.4%) of 432 marked chicks returned to the study area; most (94%) bred locally as yearlings (Table 1). Four of the 62 philopatric plovers (6.5%) were observed repeatedly during a breeding season suggesting they nested locally; however, we did not find nests for these individuals. Philopatry (of males and females combined) annually ranged from 13.0 to 16.4%. Males (17.3%) tended to be more philopatric than females (11.7%) (X^2 = 2.72, df = 1, P = 0.10). There was no gender difference in natal dispersal ($t_{26,20}$ = 0.23, P = 0.82) (Fig. 2). Female and male yearlings established first nests within northern California (RU2) at distances of 16.0 ± 29.2 km (median = 4.8, range = 0.4–125.7) and 18.2 ± 33.6 km (median = 5.0, range = 0.06–163.8), respectively, from their natal nests. Considering only the years 2001 through 2005 when we intensively monitored fledging success, 53 (31.5%) of 168 fledged chicks returned to the northern California study area.

Philopatric plovers comprised 10–22% of the local breeding population each year. Plovers bearing bands from Recovery Unit 2 have been recaptured or observed during the breeding season elsewhere along the Pacific coast (Table 2). A yearling female dispersed 474 km from the local population in 2005 to breed at Moss Landing, California after high water on the Eel River destroyed her initial nest. Another female, hatched in 2000, dispersed 354 km to breed in Oregon; she subsequently returned to breed in Humboldt

TABLE 2. Snowy Plover dispersal to breed outside of coastal northern California.

Hatch year	Gender	Breeding location	Year bred
1999	F	Siltcoos, OR	
2000	M	New River, OR	2003
2000	F	Tahkenitch, OR	2001
2000	F	Bandon, OR	2001
2001	M	Sutton Beach and Coos Bay, OR	2002–04
2001	F	New River and Bandon, OR	2003, 2005
Unknown	M	Sutton Beach, OR	2001
Unknown	M	Leadbetter Pt. and Willapa Bay, WA	2002
Unknown	M	Midway Beach, WA	2002
Unknown	F	Bandon, OR	2002
Unknown	Unk	Pt. Reyes, CA	2002
Unknown	M	Pt. Reyes, CA	2003
Unknown	Unk	Vandenberg, CA	2003
2004	F	Moss Landing, CA	2005
2004	F	Leadbetter Pt., WA	2005
2004	M	Leadbetter Pt., WA	2005
2004	M	Leadbetter Pt., WA	2005

County (2003) and Mendocino County (2004).

A greater percentage of river-hatched plovers returned to the study area (16.3% of 203 chicks) compared to beaches (7.9% of 229 hatched chicks). However, this analysis was based on chicks marked at hatch. Return rates based on fledged chicks were similar (31.0% of 58 chicks fledged from beaches; 30.0% of 110 river-fledged chicks). Most (69.4% of 49) philopatric plovers first bred in their natal habitats (i.e., beach vs. river); 30.6% (15 of 49 yearlings) switched habitats. Similar numbers of yearling males and females (n = 16 total birds) moved from their natal beach habitat to breed on the river (four males and three females), and from natal river habitat to breed on the beach (three males and five females). Two plovers (one male and one female) were absent as yearlings but returned to breed when they were 2 years of age in their natal river habitat; one male plover first bred on his natal beach as a 2-year-old.

Between-year and Within-season Dispersal.—Individuals typically moved greater distances between than within years (Table 3). There was no clear difference in the average distance moved by either males or females that were successful or failed to hatch their first clutch. There was no difference (Mann-Whitney U-test, z = 0.83, P = 0.43) in dispersal distance between two successful (10.7 ± 14.3 km) and six unsuccessful (2.3 ± 2.8 km) males or between five successful (0.4 ± 0.4 km) and four unsuccessful (118.7 ± 236.8 km) females (Mann-Whitney U-test, z = 0.37, P = 0.71).

Within a year, individuals commonly bred at a single site (yearlings and older adults combined; males: 86–100% and females: 76–90%) within the study area, rather than moving among sites (Fig. 1). This pattern was higher (4–14% annually) for males than females in each year. As yearlings, males (1.9 ± 1.0) and females (1.6 ± 0.9) bred at similar numbers of sites, and the number of breeding sites was similar as individuals bred in their second (males: 1.9 ± 1.1; females: 1.9 ± 1.2), third (males: 1.6 ± 1.2; females: 1.7 ± 1.0) or fourth year (males: 1.0 ± 0.0; females: 1.5 ± 0.7).

Migratory Movements and Winter Residency.—Most philopatric plovers were resident year-round, as evidenced by repeated observations in post-breeding and winter flocks. Fourteen of 17 philopatric males observed during winter occurred at one of several sites where flocks form near breeding areas (Clam Beach, South Spit, and at the mouth of the Eel River). Three other philopatric males wintered in southern California. Nine of 11 philopatric females (with known wintering sites) wintered locally; two wintered south of the study area. There was a tendency for individuals (males and females combined, n = 27) that hatched from early clutches to become migrants

TABLE 3. Distance (km) ($\bar{x}$ ± SD) between successive nests of male and female Snowy Plovers.

		Females		Males	
		Fate of previous nest		Fate of previous nest	
Age	Nesting attempt	Hatched (*n*)	Failed (*n*)	Hatched (*n*)	Failed (*n*)
Yearling	2nd	0.4 ± 0.4 (5)	118.7 ± 236.8 (4)	10.7 ± 14.3 (2)	2.3 ± 2.8 (6)
	3rd				0.9 ± 1.1 (4)
	4th				0.7 ± 0.8 (2)
Second Yr	1st	10.4 ± 20.4 (5)	15.4 ± 24.3 (3)	11.7 ± 20.2 (12)	1.9 ± 2.4 (5)
	2nd	2.2 ± 2.5 (2)	1.2 ± 1.5 (3)	1.0 ± 0.8 (3)	1.5 ± 1.2 (8)
	3rd		2.7 ± 2.3 (5)	0.7 ± 0.4 (4)	1.7 ± 1.9 (2)
	4th		0.9 ± 0.2 (2)		0.9 ± 0.6 (4)
	5th		23.5 ± 31.8 (2)		47.5 ± 0.0 (1)
Third Yr	1st	9.0 ± 15.8 (6)	0.2 ± 0.0 (1)	2.9 ± 4.3 (8)	2.0 ± 2.3 (2)
	2nd		2.1 ± 2.0 (5)	0.5 ± 0.6 (3)	0.8 ± 1.1 (4)
	3rd	2.8 ± 0.0 (1)	0.1 ± 0.0 (1)		1.3 ± 1.0 (3)
	4th				0.7 ± 0.6 (2)
	5th				0.6 ± 0.6 (2)
	6th				0.1 ± 0.0 (1)
Fourth Yr	1st		6.1 ± 0.0 (1)	21.2 ± 36.4 (3)	4.9 ± 0.0 (1)
	2nd				0.9 ± 0.4 (2)
	3rd				1.1 ± 0.0 (1)
	4th				2.7 ± 0.0 (1)
	5th				1.3 ± 0.0 (1)
Fifth Yr	1st			3.2 ± 0.0 (1)	

whereas individuals from later clutches were more likely to become local winter residents ($\beta = 0.05 \pm 0.03$, Wald $X^2 = 3.25$, $P = 0.07$).

DISCUSSION

Male and female Snowy Plovers in coastal northern California had similar patterns of natal dispersal and use of breeding sites; males tended to be more philopatric than females. These findings are similar to patterns from a long-term study (with a much larger sample) in central California (Stenzel et al. 2007). In the Monterey Bay area, philopatry was male biased, a pattern reported for most other shorebirds where gender differences exist. Oring and Lank (1984) concluded there was a tendency for male-biased philopatry among the 12 species of shorebirds they reviewed. Recent studies strengthen the case for male-biased philopatry. Jackson (1994) reported that males and females of three territorial shorebirds (Redshank [*Tringa totanus*], Dunlin [*Calidris alpina schinzii*], and Ringed Plover [*Charadrius hiaticula*]) breeding in the Western Isles, United Kingdom returned at similar rates and that males settled significantly nearer their natal sites than females. Pierce (1989) reported a similar finding of male settlement nearer natal sites for the Banded Dotterel (*Charadrius bicinctus*) in New Zealand. Gratto (1988) reported no gender bias in philopatry for the Semipalmated Sandpiper (*Calidris pusilla*).

The Snowy Plover has a serially polygamous, territorial mating system; males and females share incubation, but males typically care for chicks alone while females pursue additional mates (Page et al. 1995). As a consequence, during the long (~120 day) breeding season typical of the species along the Pacific coast, females may breed successfully up to three times whereas males may breed twice. The Snowy Plover occupies dynamic habitats that vary greatly in quality owing to frequent natural disturbance (e.g., tidal over-wash, river flooding, drifting sand). Coupled with high nest failure rates from predation (Page et al. 1995; Colwell et al. 2005a, 2005b), these facets place a premium on dispersal rather than being faithful to a particular nest site (Stenzel et al. 1994). We found no relationship between nesting success and breeding dispersal; a finding also reported by Stenzel et al. (1994), but in contrast to other shorebirds (Oring and Lank 1984).

Comparatively large dispersal distances of

Snowy Plovers in this study were similar to those reported by Stenzel et al. (1994, 2007) for Snowy Plovers of varying age. For both populations, the comparatively large dispersal distances may stem from two facets related to the spatial scale of study, the first methodological and the second biogeographical. First, we intensively monitored dispersal over a large area. Jackson (1994) quantified dispersal by intensively monitoring shorebirds on four study plots of 40–120 ha separated by a few km of suitable habitat, which he surveyed occasionally for dispersing birds. Jackson's (1994) study areas roughly correspond in size to each of our locations. Dispersal estimates for Snowy Plovers would have been comparable to those for Ringed Plover (1.5 and 2.4 km for males and females, respectively) had we limited the spatial scale of our study area to similar sized plots. Second, the disjunct distribution of breeding sites may have also contributed to large average dispersal distances. Average dispersal distance for both males and females approached 20 km (median distances were ~5 km and comparable to those reported by Stenzel et al. 2007). The average dispersal distance is intermediate between movements within and between locations (e.g., Clam Beach, South Spit, and gravel bars of the Eel River). Our dispersal estimates combine two groups of plovers: (1) those that would be considered truly philopatric as they returned to within a few km of their natal site, and (2) those that remained in the local area but moved in excess of 10 km to breed first at a location other than their natal site.

The breeding population of Snowy Plover in coastal northern California consists of a mix of year-round residents and migrants similar to that reported for central California (Stenzel et al. 1994). The tendency to become migratory versus resident correlated with timing of an individual's fledging in the population; chicks from late hatching clutches were more likely to become residents. Pierce (1989) reported similar findings for the Banded Dotterel. We offer the following scenario for the development of resident versus migrant behaviors in Snowy Plovers. The tendency for plovers from early and late hatching clutches to become migratory and resident, respectively, may stem from the proximity of a post-breeding flock for a juvenile to join. Specifically, chicks from early hatching clutches may become migrants because they develop a tendency to wander in search of other plovers when most adults are still breeding. In contrast, late-hatching chicks often fledge in the vicinity of post-breeding flocks, which begin to form in mid-July in our study area and elsewhere (Stenzel et al. 1994). Thus, we speculate that late season young are incorporated into what will become the wintering flock and establish their winter residency patterns. If this scenario is accurate, it may explain the increasing evidence that habitat protection for non-breeding flocks can lead to establishment of breeding plovers at wintering sites (Lafferty 2001).

CONSERVATION IMPLICATIONS

Breeding Snowy Plovers in coastal northern California are linked through dispersal with subpopulations elsewhere in the range of the listed population segment. Large dispersal distances of yearlings may be a consequence of this isolation and disjunct breeding locations. Individuals occasionally move long distances (to breed) both north and south on the Pacific coast (Stenzel et al. 1994, 2007). These large movements indicate that plovers are capable of colonizing suitable habitat throughout the species' range. The establishment of local breeders, however, may be enhanced by the presence of flocks of post-breeding plovers when fledglings search for a wintering site. The absence of a relationship between nesting success and dispersal strengthens findings of Stenzel et al. (1994) who suggested that wide-ranging movements of individuals were a consequence of the species' long breeding season, sequentially polygamous mating system, use of dynamic breeding habitats, and frequent nest failure. Individuals move widely among multiple sites within and among breeding seasons to capitalize on breeding habitat of varying quality, including the availability of mates (Stenzel et al. 1994). Wide-ranging movements suggest that plovers are capable of colonizing formerly unoccupied sites such as newly restored habitats and those areas afforded enhanced protection under the Endangered Species Act.

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JUVENILE LESSER PRAIRIE-CHICKEN GROWTH AND DEVELOPMENT IN SOUTHEASTERN NEW MEXICO

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ABSTRACT.—We examined growth rates and physical development of four body characteristics (mass, wing chord, bill length, and head width) of Lesser Prairie-chickens (*Tympanuchus pallidicinctus*) 3 to 111 days post-hatch in southeastern New Mexico. Growth rates, inflection points, and selected growth curves (logistic and Gompertz) associated with body mass and wing chord were similar between Lesser Prairie-chickens in New Mexico and Kansas. The asymptotic body mass (713 ± 7 g) was less for female and male yearling Lesser Prairie-chickens in New Mexico than for either yearling females or males in Kansas (male: 789 ± 4, female: 719 ± 6). Juvenile Lesser Prairie-chickens in New Mexico achieved 90% of their asymptotic body mass 7 days faster than Lesser Prairie-chickens in Kansas. *Received 18 October 2005. Accepted 9 October 2006.*

Most populations of prairie grouse in North America have declined alarmingly (Silvy and Hagen 2004). In particular, the population size of Lesser Prairie-chickens (*Tympanuchus pallidicinctus*) has decreased by an estimated 97% since the 1800s; there has also been a 92% reduction in the species' historic range and a 78% reduction in occupied range since 1963 (Crawford 1980, Taylor and Guthery 1980). The status of the Lesser Prairie-chicken as "warranted but precluded" for listing as threatened or endangered under the Endangered Species Act (U.S. Department of Interior 2004) warrants a clear concern over this species, and as habitat becomes more fragmented it will be necessary to consider the importance of discrete populations.

Basic natural history data have become increasingly more important for formulating prairie grouse conservation plans. Natural history data provide a baseline for detecting demographic changes due to nutrition, genetics, climate, or other extrinsic factors. Until recently, basic natural history data for Lesser Prairie-chickens, such as growth and development of juveniles were not available. Natal growth rates of Lesser Prairie-chickens have been described in Kansas at the northeastern extent of the species' distribution (Pitman et al. 2005). Thus, growth rates from the disconnected population in New Mexico may provide insight to developmental variability across the range of the Lesser Prairie-chicken. Growth and development data are essential for captive breeding efforts, evaluating development of birds considered for reintroductions, describing adaptive strategies for survival, and monitoring any changes in a population as a result of being genetically isolated.

Our objectives were to: (1) provide growth estimates at approximately equal time intervals for body mass, bill length, wing chord, and head width for juvenile Lesser Prairie-chickens in southeastern New Mexico; (2) describe growth rates of body mass and wing chord from hatch to the first breeding season; and (3) compare growth rates of Lesser Prairie-chickens between New Mexico and Kansas populations to answer questions regarding morphometric change through isolation that may only be detectable in growth analysis.

METHODS

Study Area and Chick Capturing.—Our study was conducted on 24,484 ha of relatively intact sand shinnery oak (*Quercus havardii*) habitat in southern Roosevelt County, New Mexico (33° 40′ N, 103° 06′ W) during summers in 2002 and 2003. The area was used primarily for grazing and 86% of the land was

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privately owned. Public land included 3,296 ha of prairie-chicken management areas owned by the New Mexico Game Commission. Sand shinnery oak plant communities dominated the region (Peterson and Boyd 1998). The climate was semi-arid continental with an average frost-free growing period of 200 days extending from mid-April to late October (Wright 2003).

We captured 3- to 5-day-old chicks 1.5 hrs after sunrise by locating and flushing radio-marked females. Chicks were captured by hand and two randomly selected chicks from each brood were marked with radio transmitters (Holohil Systems, Carp, ON, Canada; 0.75 g, 30-day battery life; Larson et al. 2001). If any of the radio-tagged chicks were lost (i.e., predated, transmitter failure or both), an additional chick within a brood was captured and radio-marked. We measured body mass of all captured chicks to 0.5 g using a Pesola spring scale. Calipers were used to measure bill length and head width, and a wing chord ruler was used to measure wing chords to the nearest millimeter. Bill length was measured from the edge of the cere to the tip of the bill, and head width was measured directly behind the eyes (Baldwin et al. 1931). Unflattened wing chord was measured from the distal end of the carpal joint to the tip of the longest primary (Pyle 1997).

We used long-handled nets to recapture radio-marked chicks at both 30 and 90 days post-hatch. We attempted recaptures at night at 30 and 90 days post-hatch by locating radio-marked birds and individual chicks with spotlights. Morphometrics were recorded from recaptured birds and transmitters were replaced with models that had longer life-expectancies (Holohil Systems, Carp, ON, Canada; 2.0 g, 90-day battery life [30 days post-hatch]; Telemetry Solutions, Concord, CA, USA; 15 g, 20-month battery life [90 days post-hatch]).

Statistical Analysis.—We compiled a table of age-specific means and standard errors to report growth estimates for body mass, bill length, wing chord, and head width measurements at 5- or 6-day intervals. We fitted growth curves to describe and compare growth rates to prairie-chicken body mass and wing chord measurements. We used the two most commonly applied growth equations for birds (Ricklefs 1973):

$$(1)\ \text{Gompertz:}\quad W = A\exp[-e^{-K(t-I)}] \quad \text{and}$$

$$(2)\ \text{logistic:}\quad W = \frac{A}{1 + e^{-K(t-I)}},$$

where W represents size (g or mm) at time t (days), A is the final size or asymptote, I is the inflection point at which 37% (Gompertz) or 50% (logistic) of asymptotic size is achieved, and K is a constant proportional to the overall growth rate (Ricklefs 1968, Zach and Mayoh 1982). We also report the time required to grow from 10 to 90% of the asymptotic body mass because K is not comparable directly between the Gompertz and logistic models (Ricklefs 1967). Wing chord at hatching is greater than 10% of the asymptote and we report the time required to grow from 50 to 90% ($t_{50\text{–}90}$; Pitman et al. 2005) of the asymptote for that morphometric. All modeling procedures were completed using SAS, Version 9.1 (SAS Institute, Inc. 2003). Growth data for bill length and head width are lacking in the literature and we report only means and standard errors, and not growth rates for these two morphometrics.

Measurements from known-age birds (of unknown gender) were used to fit logistic and Gompertz equations to observed body mass and wing chord length data. We pooled data across both years because of small sample sizes. Parameters (K and I) were estimated by least squares using the Marquardt algorithm. We fixed A for both morphometrics using mean values of an equal number (males: n = 16, females: n = 16) of randomly selected spring-caught yearling male and female Lesser Prairie-chickens from another ongoing study at the same site (Sutton Avian Research Center, unpubl. data). Model fit was closely examined for birds <50 days post-hatching because these models were developed primarily to describe the early growth of juvenile Lesser Prairie-chickens. Model fit often was poor for this portion of the curve (measured from residual plots) due to heterogeneous variance between birds of different ages (morphometrics were more variable for older birds). Therefore, we placed greater weight on observations from younger birds during the modeling process (Draper and Smith 1981) forcing the model to describe this portion of the curve more accurately. The model (and weighting if necessary) combination that provided the best fit (measured from residual plots and least sums of squares error) for birds <50 days post-hatching was selected as the final model.

Our models were created with non-independent observations (i.e., multiple measurements from broods and individual birds) and we used a bootstrap-resampling procedure (Manly 1998) to obtain 95% confidence intervals for each estimated parameter. We conducted 5,000 iterations where broods were resampled with replacement to match the total number of broods in the original data set. The selected model was refit to the resampled data set and all parameters re-estimated. Sampling distributions were developed for each estimated parameter and 95% bootstrap bias-corrected and accelerated (BCA) confidence intervals were taken from the resulting distributions (Pitman et al. 2005).

RESULTS

We measured body mass of 46 chicks in 15 broods, bill length of 43 chicks in 15 broods, wing chord of 43 chicks in 15 broods, and head width of 11 chicks in 4 broods. We recorded measurements from birds ranging from 3 to 111 days post-hatch. Means (± SE) were calculated at 5- or 6-day intervals (depending on sample size) for 11 growth periods prior to 111 days post-hatch (Table 1). Data were not collected at 16–24, 46–60, 66–100, and 106–110 days post-hatch.

The logistic equation best described gains in Lesser Prairie-chicken mass (Fig. 1A), whereas change in wing chord was best described with the Gompertz equation (Fig. 1B). Wing chord achieved 90% of asymptotic size 13.5 days faster than body mass using the inverse Gompertz and logistic growth equations, respectively.

DISCUSSION

The logistic and Gompertz growth equations, respectively, described body mass and wing chord growth patterns for juvenile Lesser Prairie-chickens in Kansas (Pitman et al. 2005) and for our study in New Mexico. Juvenile Lesser Prairie-chickens in New Mexico reached 90% of their asymptotic mass in few-

TABLE 1. Measurements (mean ± SE) of body mass, bill length, head width, and wing chord length for juvenile Lesser Prairie-chickens from hatch to 111 days post-hatch in southeastern New Mexico, 2002–2003. Time intervals of 5 or 6 days were used to summarize the data.

Age (days post-hatch)[a]	*n*	Mean age	Mass (g)	*n*	Mean age	Bill length (mm)	*n*	Mean age	Head width (mm)	*n*	Mean age	Wing chord (mm)
0–5	27	4.3 ± 0.2	19.4 ± 0.7	23	4.5 ± 0.1	8.7 ± 0.3	6	5 ± 0	15.3 ± 0.2	23	4.5 ± 0.1	40.1 ± 1.6
6–10	11	7.4 ± 0.4	32 ± 1.5	11	7.4 ± 0.4	10.3 ± 0.3	0	—[b]	—	11	7.4 ± 0.4	59.1 ± 1.8
11–15	2	11.5 ± 0.5	44 ± 2	2	11.5 ± 0.5	11.5 ± 0.5	0	—	—	2	11.5 ± 0.5	74.5 ± 2.5
25–30	6	28.2 ± 0.7	151.1 ± 12.1	6	28.2 ± 0.7	15.1 ± 1	3	27.7 ± 1.3	21 ± 1.5	6	28.2 ± 0.7	131.3 ± 5.1
31–35	1	31	177	1	31	16	0	—	—	1	31	140
36–40	2	36.5 ± 0.5	205 ± 41	2	36.5 ± 0.5	18.5 ± 0.5	2	36.5 ± 0.5	21.5 ± 1.5	2	36.5 ± 0.5	153 ± 11
41–45	2	42.5 ± 1.5	243 ± 18	2	42.5 ± 1.5	17.5 ± 0.5	1	41	24	2	42.5 ± 1.5	155.5 ± 3.5
61–65	0	—	—	1	61	20	0	—	—	1	61	196
101–105	2	103.5 ± 0.5	675 ± 25	2	103.5 ± 0.5	21.1 ± 1.1	2	103.5 ± 0.5	26.7 ± 1.9	2	103.5 ± 0.5	210.5 ± 9.5
111–115	1	111	770	1	111	16.9	1	111	26.4	1	111	217

[a] No data were collected from chicks between 16–20, 46–60, 66–100, and 106–110 days post-hatching intervals.

[b] Dashes indicate null values.

TABLE 2. Parameter estimates and 95% bootstrap bias-corrected accelerated confidence intervals (CI_L, CI_U) for equations describing growth of juvenile Lesser Prairie-chickens in southeast New Mexico, 2002–2003. Growth rate (*K*) and inflection point (*I*) were estimated through modeling using the logistic equation for mass and Gompertz equation for wing chord. Time (*t*) needed to grow from 10 to 90% of the asymptote is presented for mass and 50 to 90% of the asymptote for wing chord.

Morphometric variable	*K*			*I*			A^a			
	Estimate	CI_L	CI_U	Estimate	CI_L	CI_U	Estimate	CI_L	CI_U	*t*
Mass (g)	0.088	0.078	0.096	44	41	48	713	698	727	50
Wing chord (mm)	0.053	0.047	0.059	13	13	14	210	207	213	35
* Male mass (g)	0.078	0.056	0.094	48	52	55	789	—	—	57
* Female mass (g)	0.074	0.058	0.080	51	54	60	719	—	—	61

[a] All asymptotes (A) were fixed in our modeling efforts. We estimated asymptotes by arbitrarily selecting a random sample of measurements from 32 juvenile males and females captured on leks the following spring. These values were pooled across genders and years to calculate means, standard errors, and sample sizes for body mass (713 ± 7 g, $n = 32$) and wing chord (210 ± 1 mm, $n = 32$).

* Data from Pitman et al. (2005).

er days (50 days) than gender pooled (54 days) birds in Kansas. However, growth rate estimates *K* and *I* were similar (New Mexico: $K = 0.088$, $I = 44$; Kansas: $K = 0.084$, $I = 47$), indicating rates of growth are approximately the same but asymptotic body size was greater in Kansas. In comparison to Kansas, faster growth rate and smaller asymptotic mass in New Mexico are consistent with Ricklefs' (1973) hypothesis about the inverse relationship between asymptotic body size and growth rate. However, our results remain speculative but consistent with the inverse relationship hypothesis because there are no data for the estimated day of inflection. Mean body mass of spring-captured male (789 ± 4 g) and female (719 ± 6 g) Lesser Prairie-chickens in Kansas (Pitman et al. 2005) were greater than our pooled estimate (713 ± 7 g) from New Mexico, suggesting that individuals in northern latitudes achieve greater body mass than those in southern areas. Latitudinal size differences within a species could be attributed to Bergman's Rule (populations in colder climates [higher latitude] have larger bodies than populations in warmer climates [lower latitudes]). However, food availability, genetics, adaptive survival strategies, or climate could contribute to this difference.

Inflection points for wing growth, in addition to differences in asymptotic body mass between the two populations of Lesser Prairie-chickens, approximately corresponded to initial flight capabilities in juvenile Lesser Prairie-chickens as wing chord measurements were 96.5% longer in 0–5 day-old chicks in New Mexico versus Kansas. However, the average age of birds from which measurements were taken in Kansas was 0.4 days post-hatch compared to 4.5 days post-hatch in New Mexico. Wing growth inflection points from Kansas (Pitman et al. 2005) and our study (12 and 13 days, respectively) were within the range of days when Lesser Prairie-chickens first begin to fly (7–14 days depending on how flight is defined; Ricklefs 1973, Giesen 1998), indicating the rapid period of wing chord growth occurs just prior to when flight capabilities are achieved. Had wing chords been measured identically between our study (not flattened) and Pitman et al. (2005) (flattened), the inflection points for wing chord may have been the same. Other galliform researchers (Milby and Henderson 1937, Lewin 1963) have reported similar flight ages ranging from 7 to 11 days. Our conclusion, that inflection point is indicative of flight capabilities in galliforms, could not be supported as they did not provide growth inflection points.

Our study, the first on growth and development of juvenile Lesser Prairie-chickens in southeastern New Mexico, yielded broadly similar results to that of Pitman et al. (2005). However, there were slight differences as asymptotic body size was greater in Kansas. We cannot identify the source of these differences, which could range from food availability to genetics (either through drift or local adaptation). These differences, however slight, should be monitored and considered if captive breeding programs are established in an effort to repopulate areas where Lesser Prairie-chickens have been extirpated.

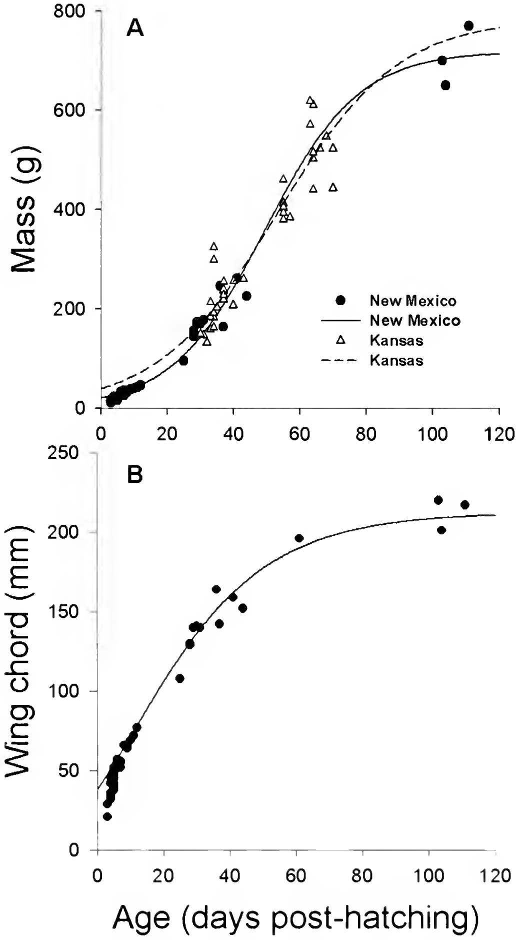

FIG. 1. Changes in Lesser Prairie-chicken body mass (A) (logistic equation, $n = 46$) and wing chord length (B) (Gompertz equation, $n = 43$) from 3 to 111 days post-hatch for birds in southeastern New Mexico, 2002–2003. Body mass of juvenile Lesser Prairie-chickens from southwestern Kansas is included in graph A (Pitman et al. 2005).

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NEST-SITE SELECTION AND NEST SURVIVAL OF NORTHERN BOBWHITE IN SOUTHERN TEXAS

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ABSTRACT.—We examined abiotic and biotic variables potentially associated with Northern Bobwhite (*Colinus virginianus*) nest-site selection and nest success in southern Texas, USA during 2002–2005. These data were used to characterize bobwhite nest-site selection, and to develop and evaluate models of daily nest survival in Program MARK. Nest sites (n = 123) had greater visual obscurity (3.50 vs. 2.60 dm) and vegetation height (64 vs. 47 cm), and less bare ground (11 vs. 25%) compared to random locations (n = 123). The two best models indicated daily nest survival increased with increasing mean maximum temperature and increasing cumulative precipitation. The model-averaged (± SE) estimate for bobwhite daily nest survival was 0.9593 ± 0.0060. These results suggest that bobwhites selected for a specific range of nest-site microhabitat attributes, but that nest predation was largely random. Bobwhite nest survival and productivity in semiarid, subtropical, southern Texas may be largely dependent on weather factors (e.g., temperature and precipitation). *Received 22 May 2006. Accepted 29 December 2006.*

Nest success is key to avian production and recruitment. Ground-nesting gamebirds in particular, including the Northern Bobwhite (*Colinus virginianus*) (hereafter, bobwhite), have high nest-loss rates (Reynolds et al. 1988, Newton 1993, Rollins and Carroll 2001). An understanding of the principal factors influencing nest success is necessary to effectively understand the population dynamics of the bobwhite.

Evolutionary theory suggests birds should select nest sites that maximize reproductive success (Wiens 1989, Martin 1993). Nest-site availability and habitat characteristics affecting nest fate are potentially valuable information for understanding population fluctuations of bobwhites in regions where nesting habitat is subject to periodic alteration by severe weather (e.g., drought and heat) (Lehmann 1984, Guthery et al. 2000, Rollins 2002) and anthropogenic influences such as grazing (Cantu and Everett 1982, Brown et al. 1993, Rollins 2002). Numerous studies have documented microhabitat (i.e., site-level) characteristics at bobwhite nests (Klimstra and Roseberry 1975, Simpson 1976, Lehmann 1984). None of the three studies that examined microhabitat characteristics of both nest sites and random sites, and between failed and successful nests (Taylor et al. 1999, Townsend et al. 2001, Lusk et al. 2006) was conducted in semiarid, subtropical, rangeland habitat of southern Texas.

Bobwhite productivity also may be influenced by weather. Drought is a recurrent feature in southern Texas and may be the driving mechanism of the characteristic boom-bust phenomenon exhibited by bobwhite populations in the region (Lehmann 1984; Hernández et al. 2002, 2007). It is becoming more apparent that reduced precipitation (Kiel 1976, Bridges et al. 2001, Hernández et al. 2005) and high temperatures (Guthery et al. 1988; Forrester et al. 1998; Guthery et al. 2001, 2005) at nest level associated with drought have significant potential to negatively impact bobwhite productivity in southern Texas.

We conducted a 4-year study of Northern Bobwhites in southern Texas to gain a better understanding of the biotic and abiotic factors influencing nest success (Rader 2006). The objectives of this paper are to: (1) describe microhabitat characteristics of nest sites versus random locations, (2) describe abiotic and biotic factors associated with successful and

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failed nests, and (3) develop and evaluate competing models of daily nest survival.

METHODS

Study Area.—The study was conducted on the San Tomas Hunting Camp (~15,000 ha) on the Encino Division of the King Ranch in Brooks County, ~32 km south of Falfurrias, Texas (26° 58′ N to 26° 50′ N, 98° 02′ W to 98° 00′ W). The area is dominated by honey mesquite (*Prosopis glandulosa*)–live oak (*Quercus virginiana*) savannah and Tamaulipan thornscrub (McLendon 1991, Fulbright and Bryant 2002, Rader 2006). Other characteristic vegetation included huisache (*Acacia smallii*), granjeno (*Celtis pallida*), prickly pear (*Opuntia lindheimeri*), tasajillo (*O. leptocaulis*), seacoast bluestem (*Schizachyrium scoparium*), gulf cordgrass (*Spartina spartinae*), purple threeawn (*Aristida purpurea*), doveweed (*Croton* spp.), sunflower (*Helianthus* spp.), and sandbur (*Cenchrus incertus*). The climate is semiarid and subtropical with periodic drought. Annual rainfall averages 56–66 cm; the annual mean temperature is ~23° C with a mean January temperature of ~9° C and a mean maximum July temperature of ~35° C (Lehmann 1984). Data collection occurred during an unusually wet period. The mean annual precipitation was 76 cm for 2002–2004 at the National Oceanic and Atmospheric Administration (NOAA) weather station in Falfurrias (U.S. Department of Commerce 2005). Major land uses included cattle grazing, petroleum extraction, and hunting, primarily for bobwhites and white-tailed deer (*Odocoileus virginianus*) (Fulbright and Bryant 2002).

The study was conducted on three distinct study sites (North Viboras, Loba, Cuates), each ~1,200–2,000 ha and separated by ≥5 km. Study sites were arranged north to south with a decreasing percentage of woody cover present at each study site (North Viboras = 32%, Loba = 11%, Cuates = 5%). Sites were representative of the range of woody cover and landscape habitat variability present on the study area.

Nest-site Selection.—We quantified bobwhite nest-site selection by comparing actual nest sites with random locations. We captured bobwhites throughout 2002–2005 at each study site using funnel traps baited with milo (Stoddard 1931) as needed to maintain ≥20 radio-marked bobwhites per site. We radio-marked a sample of bobwhites using 6–7 g, neck-loop, radio transmitters (American Wildlife Enterprises, Tallahassee, FL, USA). We used three-element, directional, hand-held, yagi antennas and portable receivers to track bobwhites approximately three times/week. We assumed bobwhites were incubating when found in the same location on two consecutive tracking attempts. Once nests were located, they were monitored every 1–2 days to ascertain nest fate. We examined the nest bowl to record fate if no bird was present at the nest.

We quantified vegetation height, visual obscurity, and canopy cover (i.e., grass, herbaceous, woody, and bare ground) at each nest site and at four random locations for each nest site once nesting had ceased. We measured vegetation height at the nest from the bottom-center of the nest bowl. We measured visual obscurity from the mean of four observations from the four cardinal directions using a Robel pole (Robel et al. 1970) placed at the center of the nest bowl or at a random location. Observations were taken at a distance of 4 m and height of 1 m. We estimated percent canopy cover at each nest and random site using a modified 1-m^2 Daubenmire frame (Daubenmire 1959). We selected random locations in each of the four quadrants of a circle within a 200-m radius of each nest-centered location. We used a random number generator to assign compass azimuth and distance to the random point in each quadrant. We took the mean of the vegetation measurements for the four random sites and used that value for comparison with each nest site. We tested for differences in vegetation height, visual obscurity, and canopy cover between nest and random sites using a Mann-Whitney test (Bradley 1968), because the data were not normally distributed.

Nest Success.—We used the Mann-Whitney test to examine differences between successful and failed nests in visual obscurity, vegetation height, bare ground, forb, grass, mean maximum temperature, and cumulative precipitation. We calculated mean maximum temperature as the mean of the maximum temperatures recorded for each day the nest was under observation. We calculated cumulative precipitation as the cumulative precipitation recorded 30 days prior to the nest being located and for each day the nest was under observation. Temperature and precipitation data were obtained from the nearest NOAA weather station in Falfurrias, Texas, ~30 km northwest of the study area. These data were intended as a coarse index of conditions in the region within the specified period and were not nest-site specific. We considered a nest was successful if ≥1 egg hatched. Failed nests included those lost to predation and abandonment. We considered a nest depredated if ≥1 egg was removed or destroyed, and the adult did not return to incubate the remainder of the clutch. A nest was considered abandoned if eggs remained intact, but incubation was not completed.

Daily Nest Survival Models.—We used the nest survival model in Program MARK (White and Burnham 1999) to evaluate competing models of bobwhite daily nest survival. Models were ranked based on Akaike's Information Criterion (AIC) (Burnham and Anderson 2002).We developed 10 *a priori* hypotheses to explain variation in nest survival. The model set incorporated constant daily nest survival (i.e., Mayfield 1961, 1975) in addition to models incorporating variation in relation to two classes of biotic covariates and four classes of abiotic covariates.

1. Microhabitat (i.e., vegetation height, visual obscurity, and percent grass). We hypothesized that increased vegetation height, visual obscurity, and percent grass would result in increased daily nest survival due to increased nest concealment from predators. Increased nest concealment should enhance nest success and bobwhites would be expected to select nest sites with greater nest concealment if this behavior maximized fitness (Martin 1993, Alcock 2001).
2. Macrohabitat (i.e., percent woody cover on the landscape). Lehmann (1984) suggested bobwhite nests may be more vulnerable to predation when placed near woody patches as many bobwhite nest predators (e.g., badger [*Taxidea taxus*], common raccoon [*Procyon lotor*], bobcat [*Felis rufus*], and gray fox [*Urocyon cinereoargenteus*]) have higher densities in wooded versus open landscapes. We predicted that increased woody cover on the landscape associated with the different study sites would result in decreased daily nest survival.
3. Temperature. We hypothesized that increased temperature during the nesting period would result in decreased daily nest survival due to nest abandonment since bobwhites would more likely experience hyperthermia when nesting during these conditions (Forrester et al. 1998; Guthery et al. 2001, 2005).
4. Precipitation. We hypothesized that increased cumulative precipitation 30 days prior to and during the nesting period would increase daily nest survival as bobwhite productivity has been linked to increased rainfall during the nesting season in southern Texas (Kiel 1976, Bridges et al. 2001, Hernández et al. 2005).
5. Date. We predicted that variation in daily nest survival would be related to temporal variation within seasons. Lehmann (1946, 1984) suggested that increased availability of alternate foods to predators as mast abundance improves later in the summer may result in increased daily nest survival.
6. Year. We predicted that year-to-year variation would explain variation in daily nest survival rates due to changing weather patterns, predator population fluctuations, etc. associated with different nesting seasons (Dinsmore et al. 2002).

RESULTS

Nest-site Selection.—We quantified microhabitat attributes at 123 bobwhite nests during 2002 (37). 2003 (44), 2004 (36), and 2005 (6). Nest sites differed from random locations for five of six microhabitat variables measured (Table 1). Nest sites had greater visual obscurity (+35%), vegetation height (+36%), and grass cover (+13%), and decreased bare ground (−56%) and forb cover (−12%) compared to random locations (Table 1). The absolute differences between nest and random locations for the forb and grass variables were small and their biological significance is questionable. Nest sites consisted largely of grass, followed by relatively even proportions of bare ground, forb, and woody cover.

Nest Success.—We found only one difference between successful and failed bobwhite nests for the variables tested (n = 109) (Table 2). The mean maximum temperature recorded

TABLE 1. Microhabitat characteristics of nest-centered (n = 123) and random locations (n = 123) for Northern Bobwhites in southern Texas, USA, 2002–2005.

	Nest-centered			Random				
Variable	Mean	SE	Range	Mean	SE	Range	U[a]	P
Visual obscurity (dm)	3.50	0.100	1.3–7.8	2.60	0.097	0.0–5.5	3,824	<0.001
Vegetation height (cm)	64.00	2.550	14–200	47.00	1.765	5–90	4,711	<0.001
Bare ground[b]	0.11	0.010	0.03–0.38	0.25	0.016	0.03–0.86	3,749	<0.001
Forb[b]	0.15	0.016	0.03–0.86	0.17	0.013	0.03–0.63	6,066	0.004
Grass[b]	0.70	0.023	0.03–0.98	0.62	0.021	0.03–0.98	5,982	0.003
Woody[b]	0.11	0.018	0.03–0.98	0.06	0.006	0.03–0.38	7,129	0.258

[a] Mann-Whitney U statistic.

[b] Proportion of total cover for this cover type.

during nest observation was 0.6° C lower for failed nests compared to successful nests. This difference is small and we cannot conclude that statistical significance equals biological significance in this case.

Daily Nest Survival Models.—The best models identified indicated that bobwhite daily nest survival increased with increasing mean maximum temperature and increasing cumulative precipitation during the nesting period (n = 109) (Table 3). These models were virtually indistinguishable, differing by <2 ΔAIC_c units and having Akaike weights of 0.398 and 0.349, respectively. Models that held daily nest survival constant (i.e., Mayfield method) or contained covariates for microhabitat, macrohabitat, date, and year had virtually no support (i.e., ΔAIC_c >4 and Akaike weights <0.05).

We plotted daily nest survival versus mean maximum temperature and cumulative precipitation, respectively for the two best models (Fig. 1). Bobwhite daily nest survival modeled as a function of mean maximum temperature alone increased from 30° to 37.6° C (Fig. 1A). Daily nest survival modeled as a function of both mean maximum temperature and cumulative precipitation showed different patterns when examined at three different levels of mean maximum temperature and cumulative precipitation, respectively. Daily nest survival versus mean maximum temperature at three levels of precipitation had the same pattern (Fig. 1A) with daily nest survival increasing with the level of cumulative precipitation (Fig. 1B). Daily nest survival versus cumulative precipitation at three levels of mean maximum temperature indicated a negligible precipitation effect at mean maximum temperature levels of 34° and 37.6° C (Fig. 1C). The model-averaged (± SE) estimate for bobwhite daily nest survival from the two best models was 0.9593 ± 0.0060.

DISCUSSION

Nest-site Selection.—Increased visual obscurity and vegetation height, and decreased

TABLE 2. Biotic and abiotic variables for successful (n = 61) and failed (n = 48) Northern Bobwhite nests in southern Texas, USA, 2002–2004.

	Successful			Failed				
Variable	Mean	SE	Range	Mean	SE	Range	U[a]	P
Visual obscurity (dm)	3.50	0.144	2.1–7.8	3.50	0.121	2.0–6.1	1,419	0.781
Vegetation height (cm)	67.00	2.831	23–116	63.00	4.125	14–138	1,242	0.175
Bare ground[b]	0.10	0.012	0.03–0.38	0.12	0.016	0.03–0.38	1,301	0.271
Forb[b]	0.17	0.024	0.03–0.86	0.14	0.025	0.03–0.63	1,305	0.292
Grass[b]	0.70	0.031	0.16–0.98	0.69	0.034	0.03–0.98	1,420	0.780
Temperature[c]	35.30	0.182	31.8–37.6	34.70	0.235	31.6–37.5	1,098	0.025
Precipitation[d]	7.80	0.650	0.70–17.5	8.00	0.830	0.80–33.0	1,461	0.985

[a] Mann-Whitney U statistic.

[b] Proportion of total cover for this cover type.

[c] Mean maximum daily temperature (°C) recorded during period nests were under observation.

[d] Cumulative precipitation (cm) recorded 30 days prior-to and during the period nests were under observation.

TABLE 3. Selection results for models of daily nest survival rate for Northern Bobwhite nests in southern Texas, USA, 2002–2004 (n = 109). Rankings were based on Akaike's Information Criterion (AIC) values.

Model[a]	K[b]	AIC$_c$[c]	ΔAIC	Weight
$\beta_0 + \beta_1$ **Temp*	2	331.40	0.00	0.398
$\beta_0 + \beta_1$ **Temp* + β_2 **Precip*	3	331.66	0.26	0.349
$\beta_0 + \beta_1$ **Precip*	2	335.26	3.86	0.058
β_0[d]	1	335.61	4.20	0.049
$\beta_0 + \beta_1$ **VegHeight*	2	336.02	4.62	0.04
$\beta_0 + \beta_1$ **VisObscurity*	2	336.64	5.24	0.029
$\beta_0 + \beta_1$ **Cuates* + β_2 **Loba* + β_3**Viboras*	4	336.68	5.27	0.028
$\beta_0 + \beta_1$ **Date*	2	337.58	6.17	0.018
$\beta_0 + \beta_1$ **Grass*	2	337.61	6.21	0.018
$\beta_0 + \beta_1$ **2002* + β_2 **2003* + β_3 **2004*	4	338.12	6.72	0.014

[a] *Temp* is the covariate mean maximum temperature; *Precip* is the covariate cumulative precipitation; *VegHeight* is the covariate vegetation height at nest; *VisObscurity* is the covariate nest visual obscurity; *Cuates*, *Loba* , and *Viboras* are covariates of study sites; *Date* is the covariate describing nesting period; *Grass* is the covariate describing grass cover at nest-sites; and *2002*, *2003*, and *2004* are the covariates for year of study.

[b] Number of model parameters.

[c] Akaike's Information Criterion corrected for small samples.

[d] Intercept-only model of constant daily nest survival rate.

bare ground appear to be consistently important features of bobwhite nest sites. We did not find that woody cover significantly influenced nest-site selection and note the nature of woody cover (e.g., species composition) in Oklahoma (Townsend et al. 2001) and in the Texas Panhandle (Lusk et al. 2006) differs from that found in our study area in southern Texas. Bobwhites in Kansas preferred nest sites with taller vegetation, greater visual obscurity, and less bare ground than random sites (Taylor et al. 1999), while those in Oklahoma selected nest sites with greater structural complexity, grass and woody cover, and less bare ground compared to random sites (Townsend et al. 2001). Bobwhite nest sites in the Texas Panhandle became more suitable with increasing nest-canopy height and shrub cover, and decreasing bare ground (Lusk et al. 2006).

Nest Success.—Bobwhite nest success was not affected by the microhabitat characteristics or weather variables measured with the possible exception of mean maximum temperature. Research on bobwhite nest success has produced ambiguous results with respect to correlations with measures of nest-site vegetation. Most studies have indicated no significant differences between successful and unsuccessful nests in terms of nest concealment (Lehmann 1946, 1984; Klimstra and Roseberry 1975; Simpson 1976; Townsend et al. 2001). However, Taylor et al. (1999) reported that successful bobwhite nest sites had less litter cover and were in habitat patches with taller grass cover. Lusk et al. (2006) established that successful bobwhite nests had higher vegetation canopies, more shrub cover, and more bare ground than unsuccessful nests. Lehmann (1984) reported nest sites that were more homogeneous (i.e., in terms of height and type of vegetation) relative to immediate surrounding vegetation had a higher probability of success.

Daily Nest Survival Models.—Models that estimated daily nest survival as a function of abiotic variables (i.e., temperature and precipitation) were best supported. This is consistent with our descriptive data (Table 2) for mean maximum temperature. Increasing precipitation during the nesting season has been shown to be positively correlated with bobwhite productivity in southern Texas (Kiel 1976, Bridges et al. 2001, Hernández et al. 2005). Our model that incorporated both temperature and precipitation covariates indicated that temperature had a constant influence on daily nest survival, but that precipitation did not (Fig. 1B, C). The lack of influence from precipitation at temperatures of ≥34° C indicates that temperature has the greatest influence on daily nest survival, which is substantiated by our descriptive data (Table 2). Lusk et al. (2002) also found that an index of bobwhite abundance increased with July and August temperature.

We found little support for models that assumed constant daily nest survival or that es-

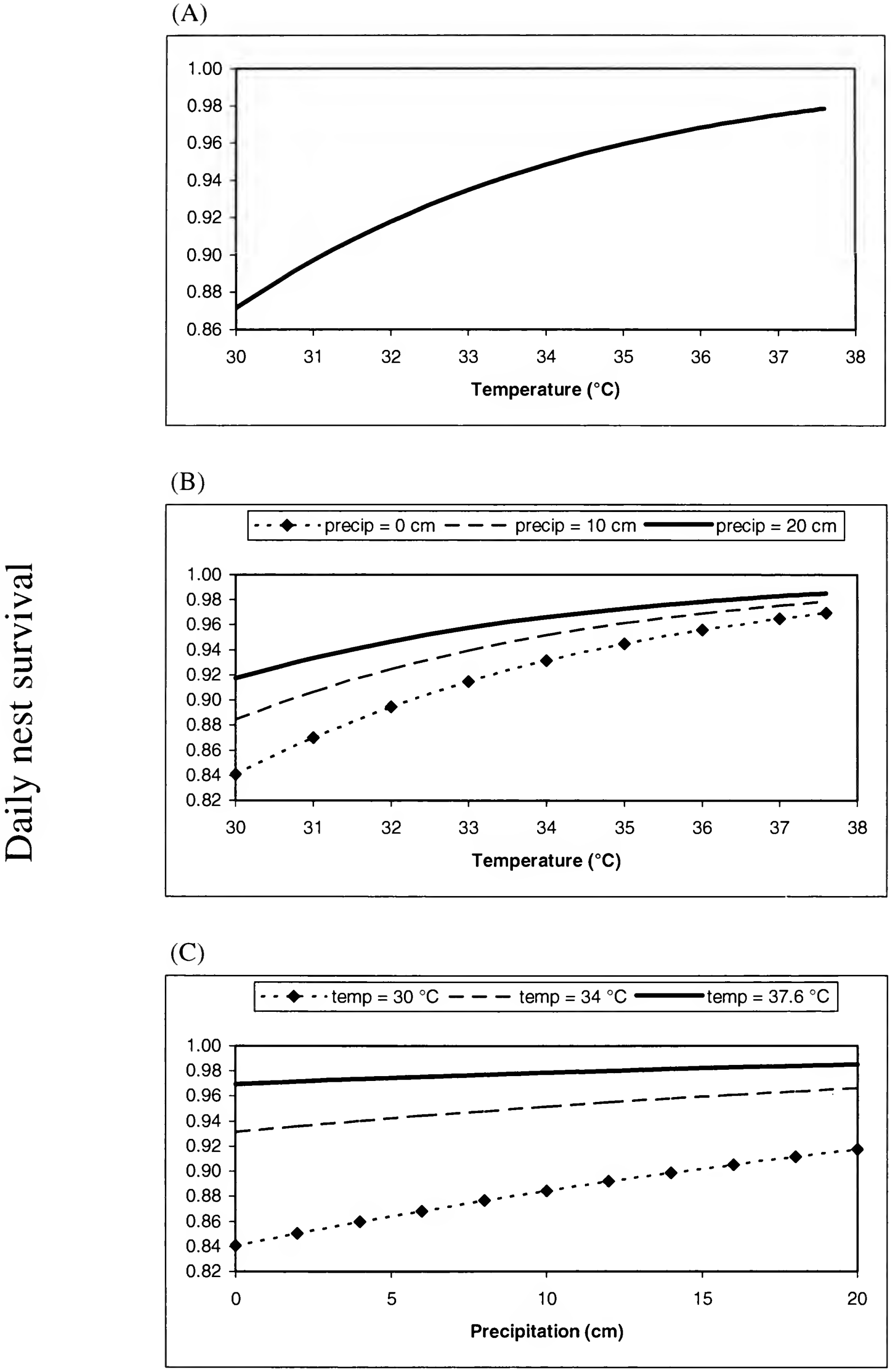

FIG. 1. Daily nest survival probabilities for Northern Bobwhites as a function of (A) mean maximum temperature, (B) mean maximum temperature at three levels of cumulative precipitation, and (C) cumulative precipitation at three levels of mean maximum temperature in southern Texas, USA, 2002–2004.

timated nest survival as a function of microhabitat, macrohabitat, date, or year. Most previous bobwhite nesting studies used apparent nesting success or Mayfield estimator derivatives to estimate nest survival and suggested that habitat (both site- and landscape-level) may have a role in nest survival (e.g., Lehmann 1946, 1984; Klimstra and Roseberry 1975; Twedt et al. 2002). Our study area was comprised of largely contiguous rangeland habitat at the landscape level and relatively high-quality nesting cover due to above-average precipitation. This may partially explain the inability of habitat covariates to show significant variation in daily nest survival. We believe habitat conditions were optimal for bobwhites during the study period and prevented measurement of the potential negative impacts of poorer habitat on daily nest survival.

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CHANGES IN BIRD COMMUNITIES AND WILLOW HABITATS ASSOCIATED WITH FED ELK

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ABSTRACT.—I assessed changes in bird distributions associated with alteration of riparian willow (*Salix* spp.) habitat by supplementally-fed elk (*Cervus elaphus nelsoni*) in western Wyoming, USA. Bird communities in stands close to (n = 4) and distant from (n = 4) feeding stations were dissimilar (complement of the Morisita-Horn index = 0.27). Stands close to feeding stations had lower species richness and relative abundances of all birds while relative abundances of all shrub-steppe species were greater, an effect of elk-induced conversion of willow to shrub-steppe habitat. Elk affected habitat mainly by reducing willow cover <2 m in height. Reductions in willow cover at >0.5–1 and >1–2 m, relative to 11 alternative variables, were responsible for declines in Willow Flycatchers (*Empidonax traillii*), MacGillivray's Warblers (*Oporornis tolmiei*), and Fox Sparrows (*Passerella iliaca*). Elk feeding in the Gros Ventre River Valley had reduced but similar effects on birds and habitat despite a smaller number of elk fed (1,900 vs. 9,200 annually for 1994–1998) and a shorter duration of feeding (initiation in 1960 vs. 1912) relative to the National Elk Refuge. These effects can extend at least 1.5 km.
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Supplemental feeding that began in 1912 has contributed to elevated densities of elk (*Cervus elaphus nelsoni*) in winter on the National Elk Refuge (NER) (Smith 2001). Both public and private feeding programs for wild ungulates have since become common (Smith 2001; EMA, unpubl. data). Habitat alteration by elk has been reported on the NER (Murie 1951, Craighead 1952, Smith et al. 2004) and is a typical consequence of high densities of native ungulates generally (Alverson et al. 1988, Brandner et al. 1990, Teer 1997). Several reports suggest that browsing by elk is the most important proximate cause of degradation and loss of willow (*Salix* spp.) habitat in Yellowstone National Park (Singer et al. 1998), where elk were fed until the 1920s, and Rocky Mountain National Park (Hess 1993).

Past studies indicate that birds are particularly sensitive to degradation of riparian areas by domestic ungulates (e.g., Saab et al. 1995, Tewksbury et al. 2002). Browsing of shrubs and trees by locally abundant wild ungulates can reduce bird abundance, diversity, and productivity (Braun et al. 1991, McShea et al. 1995, Berger et al. 2001). However, effects on birds related to feeding programs that increase densities of wild ungulates have received little critical evaluation (but see Dobkin et al. 2002).

Some bird species decline due to browsing by domestic ungulates (e.g., Willow Flycatcher [species names in Table 1]; Sedgwick 2000), but many other common species display variable responses (e.g., Yellow Warbler, Song Sparrow; Saab et al. [1995] present lists of species). The magnitude of declines in the former group and the direction of change in the latter group likely vary due to differences in variables such as ungulate density, duration and seasonal timing of use, and habitat type (Fleischner 1994, Saab et al. 1995, Tewksbury et al. 2002). The greater densities and longer durations of elk use on the NER have likely increased impacts to habitat and birds relative to most studies of domestic ungulates. Conversely, the different seasonal timing of use on the NER (i.e., winter vs. non-winter) may have moderated these effects because vegetation is dormant and at times protected by snow (Smith 2001).

My objectives were to: (1) examine whether willow structure explained bird distributions, and (2) describe how elk feeding operations affected willow structure.

METHODS

Study Area.—Study sites were on federal land in the Jackson Hole and Gros Ventre River valleys in Teton County, Wyoming, USA

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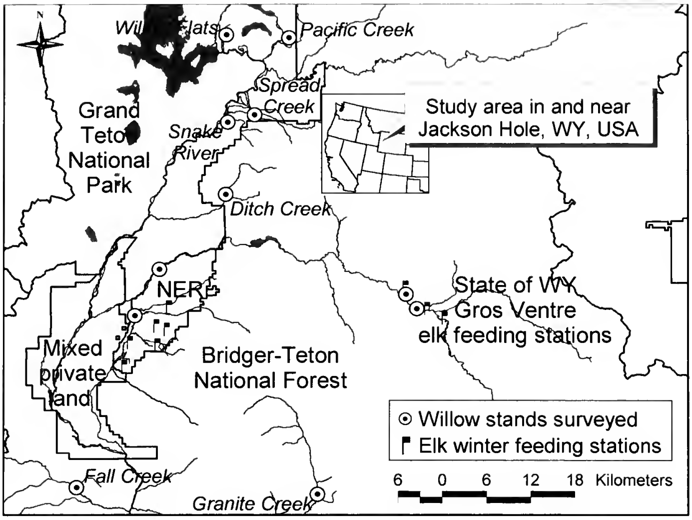

FIG. 1. Study area and sites in Teton County, Wyoming, USA. Snake River, Spread Creek, and Willow Flats were the three additional stands used in bird-habitat models.

(Fig. 1). Elevations near the southern end of Jackson Hole and the east end of the Gros Ventre River Valley are approximately 1,800 and 2,250 m, respectively. Mean temperature, precipitation, and snowfall are 14.7° C, 9.8 cm, and 0.3 cm respectively during summer (Jun–Aug), and −7.8° C, 10.2 cm, and 128.0 cm, respectively, during winter (Dec–Feb; 1948–2006; Jackson, Wyoming, Western Regional Climate Center).

I considered willow sites associated with both federal (NER) and state (Wyoming Game and Fish Department) supplemental feeding programs. The NER is administered by the U.S. Fish and Wildlife Service and has operated winter supplemental feeding stations for elk all but nine winters since inception in 1912 (Smith et al. 2004). State feeding stations considered (Alkali Creek, Fish Creek, and Patrol Cabin) are in the Gros Ventre River Valley of the Bridger-Teton National Forest. State (referred to as Gros Ventre) feeding stations were operated only during severe winters prior to 1956 and have operated nearly every year since 1960 (Boyce 1989). The approximate average number of elk fed for the years 1994–1998 was 9,200 for the NER and 1,900 for the three Gros Ventre sites combined (Smith 2001).

Study Design.—I reduced the influence of factors other than elk on habitat and birds by selecting willow stands with the following criteria: (1) dominance by tall willow species (i.e., those typically attaining heights >2 m), (2) adjacent habitat mainly shrub-steppe dominated by sagebrush (*Artemisia* spp.), (3) mean slope less than 4°, and (4) little use in the past ~50 years by domestic ungulates or moose (*Alces alces*; as verified by reports and observations of federal and state biologists).

Ungulate density at the stand scale has been used to infer effects of wild ungulates on habitat and birds (DeCalesta 1994), but is not available for my study area. I used two alternative techniques to evaluate effects of fed elk. First, I compared bird communities, elk use, and habitat structure between stands close (<5 km) to feeding stations (two stands in the NER and two stands adjacent to Gros Ventre feeding stations) and stands distant (16–36 km) from feeding stations (Ditch Creek, Fall Creek, Granite Creek, Pacific Creek; Fig. 1). The locations of NER and Gros Ventre feeding stations have changed little over time (Smith 2001). Thus, proximity to these stations should be an appropriate metric of long-term effects of elk feeding on habitat. Habitat alteration by moose in this area occurs primarily in Grand Teton National Park (Berger et al. 2001); only the Pacific Creek stand is in this park and the area I considered had little evidence (fecal pellets, tracks) of moose pres-

TABLE 1. Habitat and bird comparisons between willow stands close to (n = 4) and distant from (n = 4) elk feeding stations. All bird data are for mean detections per 35-m survey point.

	Mean (SE)		
	Stands close	Stands distant	$F_{1,6}$ (P)
Elk use measures			
Willow annual segments browsed (%)	88.2 (7.1)	28.5 (5.9)	41.71 (<0.001)
Willow <0.6 m tall browsed (%)	95.8 (4.3)	55.0 (11.7)	10.67 (0.017)
Habitat measures			
Willow height (m)	1.4 (0.4)	1.9 (0.3)	1.24 (0.31)
Grass cover (%)	64.9 (6.1)	27.1 (6.8)	17.17 (0.006)
Forb cover (%)	11.1 (2.1)	15.8 (5.0)	0.77 (0.41)
Bare ground cover (%)	2.1 (1.0)	5.9 (0.7)	10.33 (0.018)
Stagnant water cover (%)	0.5 (0.4)	1.0 (0.5)	0.49 (0.51)
Flowing water cover (%)	0.4 (0.4)	1.1 (0.4)	1.47 (0.27)
Bird community measures			
Total relative abundance	8.5 (1.8)	14.6 (1.4)	7.39 (0.035)
Species richness	5.7 (1.0)	8.7 (0.2)	8.19 (0.029)
Shrub-steppe bird relative abundance[a]	2.4 (0.5)	0.1 (0.03)	23.93 (0.003)
Bird species relative abundance[b]			Proximity effect (95% CI)[c]
Calliope Hummingbird (*Stellula calliope*)	0.0 (0.0)	0.7 (0.4)	−1.2 (−2.7, 0.3)
Willow Flycatcher (*Empidonax traillii*)	0.1 (0.1)	0.8 (0.3)	−1.7 (−3.3, −0.1)
Dusky Flycatcher (*E. oberholseri*)	0.2 (0.1)	0.6 (0.3)	−1.0 (−2.5, 0.5)
American Robin (*Turdus migratorius*)	0.2 (0.1)	0.2 (0.1)	−0.1 (−1.5, 1.3)
Gray Catbird (*Dumetella carolinensis*)	0.0 (0.0)	0.3 (0.1)	−1.3 (−2.9, 0.2)
Yellow Warbler (*Dendroica petechia*)	1.5 (0.5)	2.9 (0.4)	−1.3 (−2.9, 0.2)
MacGillivray's Warbler (*Oporornis tolmiei*)	0.03 (0.03)	1.5 (0.5)	−1.9 (−3.5, −0.2)
Common Yellowthroat (*Geothlypis trichas*)	0.4 (0.3)	1.1 (0.7)	−0.6 (−2.0, 0.9)
Fox Sparrow (*Passerella iliaca*)	0.1 (0.1)	1.0 (0.3)	−1.8 (−3.5, −0.2)
Savannah Sparrow (*Passerculus sandwichensis*)	0.9 (0.4)	0.0 (0.0)	1.4 (−0.2, 2.9)
Lincoln's Sparrow (*Melospiza lincolnii*)	1.5 (0.8)	0.9 (0.5)	0.4 (−1.0, 1.8)
Song Sparrow (*M. melodia*)	1.0 (0.4)	2.2 (0.5)	−1.3 (−2.8, 0.3)
Vesper Sparrow (*Pooecetes gramineus*)	0.3 (0.3)	0.0 (0.0)	0.6 (−0.8, 2.0)
White-crowned Sparrow (*Zonotrichia leucophrys*)	0.3 (0.1)	0.4 (0.3)	−0.4 (−1.8, 1.0)
Brewer's Blackbird (*Euphagus cyanocephalus*)	0.7 (0.7)	0.0 (0.0)	0.7 (−0.8, 2.1)
Brown-headed Cowbird (*Molothrus ater*)	0.4 (0.1)	0.7 (0.2)	−1.0 (−2.4, 0.5)

[a] Shrub-steppe birds include: Brewer's Sparrow (*Spizella breweri*), Savannah Sparrow, Vesper Sparrow, Bobolink (*Dolichonyx oryzivorus*), Western Meadowlark (*Sturnella neglecta*), Red-winged Blackbird (*Agelaius phoeniceus*), and Brewer's Blackbird.

[b] Bird species detected rarely (i.e., more than a single observation for each group of stands, yet mean detections <0.2) followed by proximity effects (with 95% CI) include: Wilson's Warbler (*Wilsonia pusilla*) 0.8 (−0.7, 2.2), Brewer's Sparrow 0.6 (−0.9, 2.0), Bobolink 0.6 (−0.8, 2.0), Western Meadowlark 0.6 (−0.8, 2.0), and Red-winged Blackbird 1.1 (−0.4, 2.5).

[c] Proximity effects are changes in species abundance related to proximity to elk feeding stations (i.e., stands close to and distant from elk feeding stations are the treatment and control groups, respectively).

ence. Granite Creek is a tributary of the Hoback River (a tributary of the Snake River). All other stands are on tributaries of the Snake River and are dominated by *Salix boothii* and *S. geyeriana*. The approximate densities of willow species that rarely attain 2 m in height (*S. wolfii*, *S. lemmonii*, and *S. planifolia*) are lower and similar among all stands except Granite Creek, which is dominated by *S. wolfii* and *S. boothii*. The greater presence of *S. wolfii* on Granite Creek may bias downwards my estimates of elk effects on willow height and cover >1 m. All *Salix* specimens were identified by R. D. Dorn following Dorn (2001).

I modeled relationships between elk use (i.e., browse rate) and habitat structure, and between habitat structure and bird abundance as a second test of elk-feeding effects. Browse rate was the percentage of annual segments browsed excluding the current year's growth on willow stems >1 cm in diameter (described further in *Habitat Surveys*). I interpreted a significant relationship between browse rate and a habitat variable across the above eight willow stands to suggest influence of elk on the habitat variable.

I used a two-step approach to evaluate the influence of elk feeding on individual bird species. First, I considered effect sizes on species abundance due to proximity to elk feeding stations (i.e., stands close to and distant from elk feeding stations constitute the treatment and control groups, respectively). Second, I developed habitat models for the four species with the greatest and four species with the smallest absolute effect sizes to evaluate the likelihood that elk have influenced effect sizes. Variation in the abundance of species with large effect sizes (species predicted to be more sensitive to elk use) should be explained by habitat variables influenced by elk. Conversely, species with small effect sizes (species predicted to be less sensitive to elk use) should be related to habitat variables over which elk have little influence or that were not controlled for during stand selection. I included in these models three additional stands in Grand Teton National Park (Fig. 1). Moose may have altered willow structure in these three stands, but their inclusion in the habitat models seems acceptable because I was interested in the relationship between bird distributions and habitat variables.

I tested for differences in browse rate, and in bird and habitat variables between the NER and Gros Ventre feeding areas to examine the importance of feeding characteristics (i.e., number of elk, years since feeding began). I also considered the relationship between browse rate and distance to the nearest feeding station to examine the spatial extent of feeding effects.

Bird Surveys.—I used 35-m radius point counts for bird surveys (Ralph et al. 1995). Each count lasted 20 min and each point was visited on three occasions in 2001 (19 May–4 Jul) over which species detections were averaged. I randomly located five points in each stand (the maximum number possible provided the smallest willow stand area) over which all bird measures were averaged. I continuously mapped locations of birds to avoid counting individuals more than once. Shrub-steppe birds were those species that nest in grassland and low shrub habitat, as well as species that typically nest in riparian habitat lacking significant willow structure (Table 1). Red-winged Blackbirds nest in willow as well as in non-woody emergent vegetation. Brewer's Blackbirds nest in willow and non-riparian shrubs. Both blackbird species were included in the shrub-steppe guild because they were observed almost exclusively within survey plots lacking substantial willow structure (Anderson 2002). I used the Morisita-Horn index (Dobkin et al. 1998) to measure community similarity between stands close to and distant from feeding stations. The complement of this index ranges from 0 (no similarity) to 1 (complete similarity).

Habitat Surveys.—All habitat variables were measured from 12 standardized locations within each 35-m radius bird survey point. I measured the distance to the center of the nearest willow shrub and its maximum height at each location, and used the point-centered quarter method to estimate stand density of willow shrubs (Bonham 1989). I recorded foliage volume at each location using the stacked cube method (Kus 1998). This involved recording percent cover for willow and for a class of other shrubs (almost exclusively shrubby cinquefoil [*Dasiphora floribunda*]) within a 1-m^2 sampling column at 0–0.5, >0.5–1, >1–2, and >2 m height classes. I also recorded within these 1-m^2 plots: cover <0.5 m of grasses, forbs, bare ground, stagnant water, and flowing water. Cover classes were: <1, >1–10, >10–25, >25–50, >50–75, >75–90, and >90%.

I documented two measures of browse use from each of the 12 locations. First, I located on the nearest willow shrub the northern-most and southern-most stems with diameter >1 cm and height 0.5–2 m (the approximate height range available in winter to browsing wild ungulates; Keigley and Frisina 1998). I then recorded browse rate on each of these two stems by cover classes. Second, if the closest willow was <0.6 m in height, I recorded only whether it had been browsed. These measures were strongly correlated ($R = 0.82$, $P = 0.013$). Thus, only browse rate was used as a metric of elk use of each willow stand.

Statistical Analyses.—I conducted statistical analyses using JMP 5.0.1 (SAS Institute Inc. 2002). I used one-way analysis of variance

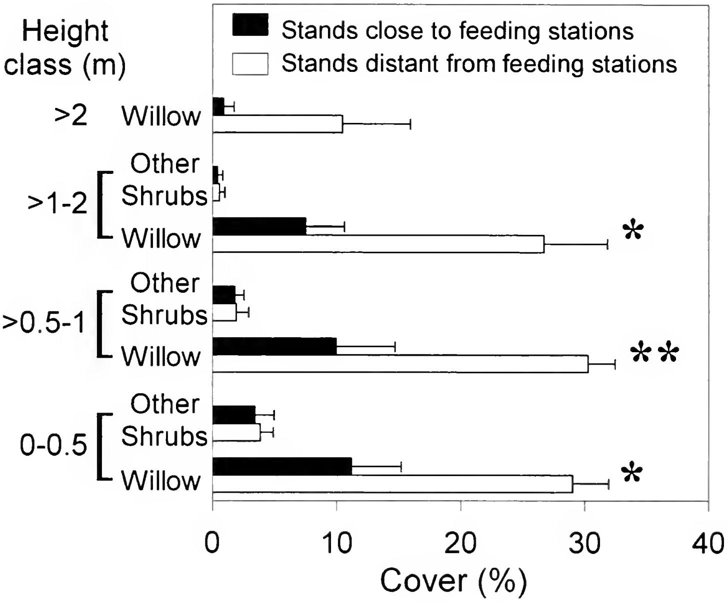

FIG. 2. Mean (+SE) cover of willow and other shrubs at multiple heights in stands close to (n = 4) and distant from (n = 4) elk feeding stations. Other shrubs were absent above 2 m (*$P < 0.05$; **$P < 0.01$).

(ANOVA) to test for differences between two means and Duncan's Multiple Range Test for pairwise comparisons among three means. I used the Welch-Satterthwaite degrees of freedom modification when variances were not homogeneous (Johnson 1995). Levene's Test was used to evaluate variance homogeneity. I used unbiased corrections to estimate effect sizes for bird species based on pooled standard deviations (Hedges and Olkin 1985). I used simple linear regression to test relationships between browse rate and habitat variables. Tests were considered significant when $P < 0.05$.

I used forward stepwise regression (considered appropriate for exploratory purposes; Hosmer and Lemeshow 1989) to model bird associations with habitat variables across all stands (n = 11). I began model development for each species by considering all univariate habitat models. Variables significant at $P <$ 0.25 were retained for further model development (Hosmer and Lemeshow 1989). I then constructed correlation matrices to detect multi-collinearity. I retained the variable that was most biologically relevant or had the lowest P-value in univariate analyses (when biological relevance was not clear) for each pair of strongly correlated ($R > 0.60$) variables. All remaining variables were included in the forward stepwise procedure. Criteria for entry and removal were $P = 0.25$ and $P = 0.10$, respectively.

RESULTS

Stands close to elk feeding stations had a higher mean browse rate and a higher mean percentage of browsed shrubs <0.6 m in height (Table 1). Mean willow cover was lower in stands close to feeding stations for the height classes 0–0.5 ($F_{1,6}$ = 12.93, P = 0.011), >0.5–1 ($F_{1,6}$ = 15.18, P = 0.008), and >1–2 m ($F_{1,6}$ = 10.33, P = 0.018), and non-significantly lower for the height class >2 m ($F_{1,3.1}$ = 2.99, P = 0.18; Fig. 2). Willow shrub height (Table 1) and cover at all height classes for non-willow shrubs (Fig. 2) did not differ among groups of stands. Grass cover was greater and bare ground lower in stands close to feeding stations, while cover of forbs, stagnant water, and flowing water did not differ between groups (Table 1). Elevation ($\bar{x}$ ± SE) did not differ between groups of stands (close 2,100 ± 85 m; distant 2,061 ± 52 m; $F_{1,6}$ = 0.15, P = 0.71), nor was it related to browse rate (R = 0.30, P = 0.47).

I observed 1,743 individual birds within 35-m radius survey points. Total relative

TABLE 2. Regressions of mean habitat variables on browse rate across willow stands ($n = 8$).

Response variables (stand means)	Coefficient (SE)	r^2	$F_{1,6}$ (P)
Willow density (per ha)[a]	−0.26 (0.52)	0.04	0.25 (0.64)
Willow height (m)	−0.01 (0.01)	0.35	3.20 (0.12)
Willow cover 0–0.5 m (%)	−0.28 (0.08)	0.69	13.14 (0.011)
Willow cover >0.5–1 m (%)	−0.30 (0.09)	0.65	11.39 (0.015)
Willow cover >1–2 m (%)	−0.28 (0.10)	0.55	7.19 (0.036)
Willow cover >2 m (%)	−0.15 (0.09)	0.32	2.84 (0.14)
Other shrub cover 0–0.5 m (%)	0.001 (0.03)	<0.01	<0.01 (0.97)
Other shrub cover >0.5–1 m (%)	−0.0002 (0.02)	<0.01	<0.01 (0.99)

[a] Relationship improved by removal of one observation ($r^2 = 0.70$, $F_{1,5} = 11.41$, $P = 0.020$).

abundance and species richness were lower and relative abundance of shrub-steppe species was greater in stands close to feeding stations (Table 1). The complement of the Morisita-Horn index was low (0.27) indicating little similarity in bird communities between groups of stands.

Increased proximity to elk feeding stations had a negative effect on the relative abundance of most willow-associated species; for Willow Flycatchers, MacGillivray's Warblers, and Fox Sparrows these negative effects were significant (i.e., 95% confidence intervals for effect sizes do not overlap zero; Table 1). Calliope Hummingbirds and Gray Catbirds were not recorded in stands close to feeding stations. Increased proximity to feeding stations had a positive effect on the relative abundance of all shrub-steppe species. None of these positive effects was significant, but all shrub-steppe species except Brewer's Sparrows were observed exclusively within stands close to feeding stations.

Browse rate was unrelated to willow height, willow cover >2 m, and cover of non-willow shrubs across stands (Table 2). Browse rate was negatively related to willow density when a single observation was removed. Browse rate was also negatively related to willow cover for 0–0.5, >0.5–1, and >1–2 m height classes. Models best explaining abundance of four species (Table 3) predicted to be more sensitive to elk use included mainly willow cover at 0–0.5, >0.5–1, and >1–2 m height classes. Only abundances of Common Yellowthroats and White-crowned Sparrows, of the four species predicted to be less sensitive to elk use, were modeled best using habitat variables cor-

TABLE 3. Models of bird species[a] abundance with habitat variables[b] across all stands ($n = 11$). Forward stepwise regression was used to develop a model for each species from a reduced set of habitat variables.

	Models[c]	r^2	F (P)
Species predicted to be more sensitive to elk use[a]			
Willow Flycatcher	Willow3 (2.27*)	0.36	5.17 (0.049)
MacGillivray's Warbler	Willow2 (3.77**) Other1 (2.08)	0.70	9.45 (0.008)
Fox Sparrow	Willow3 (4.36**)	0.68	18.97 (0.002)
Savannah Sparrow	Willow1 (−2.05)	0.32	4.21 (0.071)
Species predicted to be less sensitive to elk use[a]			
American Robin	Height (2.64*) Elevation (−1.48)	0.54	4.79 (0.043)
Common Yellowthroat	Willow1 (2.09)	0.33	4.37 (0.066)
Lincoln's Sparrow	Other2 (−5.15***) Elevation (4.59**)	0.88	28.51 (<0.001)
White-crowned Sparrow	Elevation (4.86**) Other2 (2.79*) Willow3 (2.24)	0.87	15.08 (0.002)

[a] Species predicted to be more and less sensitive to elk use are those with the largest and smallest absolute effect sizes on abundance due to proximity to elk feeding stations.

[b] Habitat variables considered include: Willow1, 2, 3, 4 (mean % willow cover at 0–0.5, >0.5–1, >1–2, and >2 m height classes, respectively); Other1, 2 (mean % non-willow shrub cover at 0–0.5 and >0.5–1 m height classes, respectively; non-willow shrub cover was usually absent above 1 m); Density (mean for willow shrubs [per ha]); Height (mean for willow shrubs [m]); Grass, Bare ground, Stagnant water, Flowing water (mean % cover <0.5 m); Elevation (m).

[c] Variables included in each model are presented with the t-statistic comparing model performance with and without the variable (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

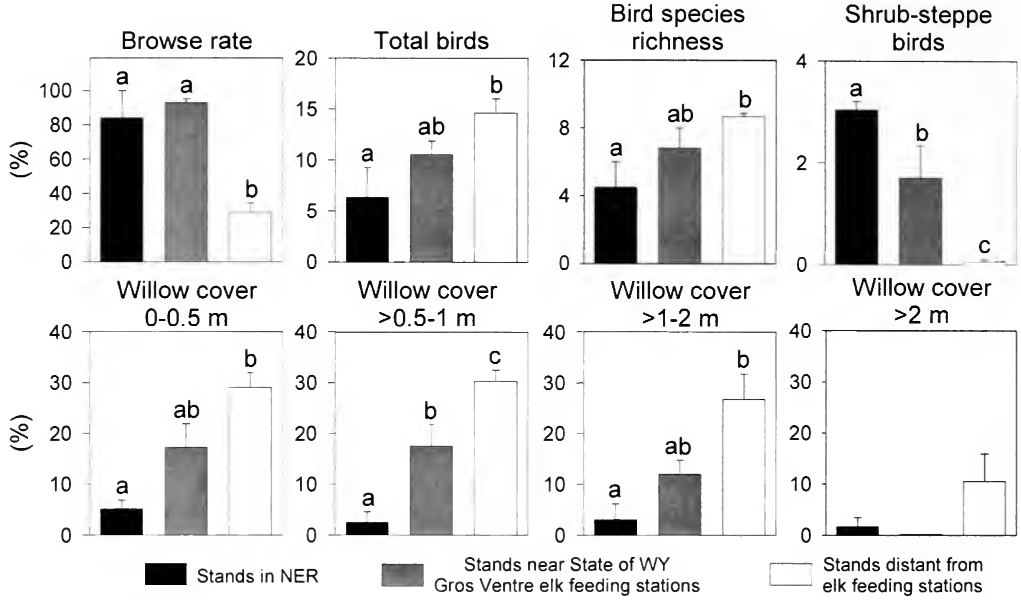

FIG. 3. Mean browse rate, bird, and habitat variables (+SE) in willow stands in the National Elk Refuge ($n = 2$), stands near State of Wyoming Gros Ventre elk feeding stations ($n = 2$), and stands distant from elk feeding stations ($n = 4$). All bird data are for mean detections per 35-m survey point. Different letters denote different groupings ($P < 0.05$).

related with browse rate. Models for these two species, however, did not perform significantly better due to inclusion of habitat variables correlated with browse rate.

NER and Gros Ventre stands had similar browse rates. However, Gros Ventre stands were consistently intermediate to stands distant from feeding stations and NER stands in bird community variables and in willow cover (Figs. 3, 4).

DISCUSSION

Elk reduced willow structure near feeding stations, which promoted reductions in the combined relative abundance of all bird species and increases in all shrub-steppe species. Experimental data on the NER (i.e., ungulate exclosures) indicate a causal relationship between elk feeding and reductions in willow structure (Smith et al. 2004). Historical observations on the NER indicate that impacts to habitat are the result of aggregating elk through supplemental feeding as opposed to normal use of historical winter range of high quality (Preble 1911, Murie 1951, Craighead 1952).

The most prominent effect of elk on habitat was to reduce willow cover <2 m in height. Domestic ungulates induce similar changes to the horizontal structure of willow (Knopf et al. 1988). Sensitivity to browsing by livestock has been documented in three species that appear to be particularly sensitive to habitat alteration by elk: Willow Flycatchers (Sedgwick 2000), MacGillivray's Warblers, and Fox Sparrows (Saab et al. 1995, Tewksbury et al. 2002).

Birds least sensitive to elk use were either habitat generalists (American Robin) or nest mainly on or near the ground: Common Yellowthroat (Guzy and Ritchison 1999), White-crowned Sparrow (Chilton et al. 1995), and Lincoln's Sparrow (Ammon 1995). Declines in species nesting on or near the ground often follow livestock grazing (Saab et al. 1995). Such declines may not be prominent in this case because elk use these willow stands in winter when snow often protects low vegetation (Smith 2001). My results indicate elk reduced mean willow cover <0.5 m in height. Thus, if snow does protect willow it is likely either uncommon or occurs at a lower height range. MacGillivray's Warblers and Fox Sparrows nest in shrubs and on the ground sug-

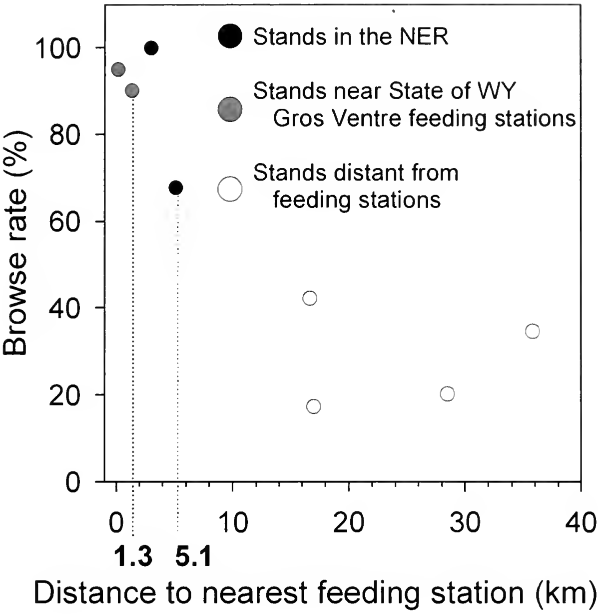

FIG. 4. Relationship of mean browse rate with distance to the nearest elk feeding station. Browse rate was highly correlated with willow cover <2 m and is used as an index of ecological effects of elk feeding.

gesting factors in addition to available nesting habitat may influence sensitivity to elk browsing. For instance, Fox Sparrows forage on the ground under dense cover (Weckstein et al. 2002). The small number of willow stands sampled and consideration of a single breeding season likely contributed to the small effect sizes and limit the resolution of the habitat models.

The willow structure and bird communities near the Gros Ventre feeding stations suggest effects of browsing (Fig. 3) despite a much smaller number of elk fed relative to the NER (1,900 vs. 9,200 annually for 1994–1998). The similar browse rates in these feeding areas despite a shorter duration of feeding in the Gros Ventre (initiation in 1960 vs. 1912) suggest bird and habitat changes could equal or exceed those in the NER. This finding may be the result of greater proximity of Gros Ventre stands to feeding stations (Fig. 4). Evidence from Gros Ventre stands indicates 1.3 km is not sufficient to reduce browse rates and effects on habitat and birds (Figs. 3, 4). The >5 km needed to reduce browse rates in the NER may not be applicable to most feeding programs given the scale of NER feeding.

The NER South stand indicates the potential extent of habitat alteration following a long duration of feeding and close proximity (<3 km) to feeding stations; tall willow structure is nearly absent. The persistence of willow sprouts or seedlings, presence of tall willow "skeletons" and stumps, abundance of tall willow in elk exclosures, and historical photos all indicate a tall willow community previously existed in this area (Smith et al. 2004). The high browse rates in this stand suggest elk eliminated willow structure by preventing replacement of tall willow shrubs.

Several factors increase the relevance of my findings. First, abundant yet non-fed populations of elk in the Intermountain West have likely produced similar changes in bird communities (e.g., Hess 1993, Singer et al. 1994). Second, MacGillivray's Warblers appear highly sensitive to elk use and, unlike most western riparian birds, are neither distributed continent-wide nor are they an eastern species with a range extension (Knopf 1986); long-term surveys of this species may be a critical component of monitoring feeding effects. Third, willow and aspen (*Populus tremuloides*) support greater diversity of flora and fauna than most habitats in this region. Thus, feeding-induced impacts to willow and aspen

(Anderson 2002) may reduce diversity at the landscape scale. Finally, wild ungulate feeding is common (Smith 2001, Peek et al. 2002) and even small, private feeding programs likely affect habitat and birds. Wild ungulates continue to browse vegetation when supplemental feed is available (Schmitz 1990) and can have dramatic effects on habitat at densities as low as four animals per km^2 (Alverson et al. 1988).

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SEASONAL FOREST-PATCH USE BY BIRDS IN FRAGMENTED LANDSCAPES OF SOUTH-CENTRAL PENNSYLVANIA

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ABSTRACT.—We surveyed birds during breeding, migratory, and wintering seasons in forest patches of two fragmented landscapes in the Valley and Ridge Province of south-central Pennsylvania during 1994–1996. Our objective was to examine presence of species in relation to forest-patch size (<2, 6–20, 40–150, and >1,500 ha) and extent of regional fragmentation. Several species, particularly long-distance migrants (e.g., Eastern Wood-pewee [*Contopus virens*], Red-eyed Vireo [*Vireo olivaceus*], Wood Thrush [*Hylocichla mustelina*], Worm-eating Warbler [*Helmitheros vermivorum*], and Scarlet Tanager [*Piranga olivacea*]), were more likely to occur in larger forest patches than in smaller patches during the breeding and spring-migratory seasons. Short-distance migrants (e.g., American Robin [*Turdus migratorius*], Gray Catbird [*Dumetella carolinensis*], and Eastern Towhee [*Pipilo erythrophthalmus*]), responded to fragmentation at a regional scale and were more commonly encountered in the more fragmented landscape, particularly during migratory periods. Species observed during fall migration were not influenced by patch size. The Pileated Woodpecker (*Dryocopus pileatus*) responded positively to patch size in all seasons, whereas the Song Sparrow (*Melospiza melodia*) was influenced negatively by patch size in three of four seasons. More research should be conducted at sites during winter and migration to corroborate these results and to examine the role patch size may have in long-term survivorship of migratory birds. *Received 26 March 2006. Accepted 9 October 2006.*

Many studies have focused on the effects of forest fragmentation on distribution of breeding birds with some species occurring more frequently in larger patches than in smaller patches (e.g., Galli et al. 1976, Butcher et al. 1981, Van Buskirk 1985, Martin 1988, Robbins et al. 1989, Dawson et al. 1993, Yahner 2000). However, fewer studies have examined the relationships between bird distribution and patch size in other seasons (but see Martin 1980; Yahner 1981, 1983; Blake 1983, 1986, 1987; Morrison et al. 1986), even though constraints on habitat use may shift among seasons. For example, during the breeding season, forest fragmentation in the northeastern and midwestern United States results in higher rates of nest predation and nest parasitism in small forest patches (Brittingham and Temple 1983, Haskell 1995, Hoover et al. 1995, Robinson et al. 1995). This pattern may result in decreased population densities of birds (Schmidt 2003). These constraints are removed during other seasons. In contrast, birds may respond more to food availability (Saunders et al. 1991, Burke and Nol 1998), site microclimate (Petit et al. 1985), and intra- and interspecific interactions that may lead to differential habitat use during migratory and winter seasons. Thus, species may shift habitats or generalize habitat use to take advantage of resources or microclimates that were unsuitable during the breeding season.

Researchers recently have considered habitat patterns during multiple seasons, attempting to link survivorship, success, and population trends in breeding and wintering areas (Marra et al. 1998, Hobson 2005). This trend has overlooked patterns during migration (Mehlman et al. 2005), although birds may be most vulnerable during the unpredictable migratory period (Sillett and Holmes 2002). Therefore, studying stopover habitat use, in addition to use of breeding and wintering habitat, may help identify seasonal shifts not evident from single-season studies.

This study investigates seasonal presence of bird species in relation to forest-patch size in south-central Pennsylvania. Specifically, we wanted to identify which species responded to patch size and if these responses differed among seasons. A second objective was to examine the influence of landscape fragmentation on seasonal presence of bird species. The matrix of the habitat in this study was pri-

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marily agricultural land (Keller 2001) and the amount of forested habitat differed significantly. We wanted to investigate if species responded to forest fragmentation consistently given the potential impact of landscape-level factors on breeding (Howell et al. 2000) and wintering (Pearson 1993) bird species, and predator loads (Heske et al. 1999).

METHODS

Study Areas.—This study was conducted from May 1994 to May 1996 in the Valley and Ridge Province of south-central Pennsylvania in two physiographic sections that vary in amount of forest fragmentation: Great Valley (Cumberland and Franklin counties) and Appalachian Mountain (Perry and Juniata counties). The parallel ridges are approximately 600–700 m in elevation and oriented southwest to northeast (Rhoads and Klein 1993). Valleys are dominated by crop production and pasture with isolated patches of deciduous forest (Yahner 2003). Forest patches were composed primarily of oak (*Quercus* spp.), hickory (*Carya* spp.), and maple (*Acer* spp.) overstory trees. The Appalachian Mountain Section (the less fragmented landscape) had a higher percent of forested habitat (40 vs. 15%), narrower valleys (1–5 vs. 5–10 km wide), and generally larger forest patches than the Great Valley Section (the more fragmented landscape). Vegetation characteristics and elevations of study sites did not differ based on patch size or physiographic section (Keller 2001).

Site Selection.—We identified deciduous-forest patches ≥0.25 ha in the valleys of Cumberland, eastern Franklin, Perry, and southern Juniata counties using 7.5-min topographic maps and 1:40,000 black-and-white aerial photographs. We minimized habitat heterogeneity and reduced confounding factors when considering potential study sites. We chose patches between 100 and 350 m in elevation, ≥50 m from other forest patches (separated by agricultural fields, pastures, maintained powerline rights-of-way, or primary or secondary roads), devoid of major disturbances (e.g., cattle grazing or logging), and with similar age (70–90 years) and structure. A maximum of eight sites in each of four size classes (small [<2 ha], medium [6–20 ha], large [40–150 ha], and extra-large [>1,500 ha]) were selected randomly in each of the two landscapes. We selected a total of 19 sites in the Great Valley Section (8 small, 6 medium, 3 large, and 2 extra-large) and 22 sites in the Appalachian Mountain Section (8 small, 7 medium, 5 large, and 2 extra-large) during 1994–1995 and 17 sites in the Great Valley Section (8 small, 4 medium, 3 large, and 2 extra-large) and 19 sites in the Appalachian Mountain Section (6 small, 6 medium, 5 large, and 2 extra-large) during 1995–1996.

Bird Surveys.—We surveyed birds within each forest patch using 15-min unlimited-radius point counts. Each patch contained two sampling points, one 50 m from the southern edge of the patch and the other 300 m from the southern edge of the patch. We maximized distance between points for small patches (<2 ha), but remained at least 25 m from an edge. Care was taken to avoid counting the same bird twice. Points were visited twice in each of four seasons for 2 consecutive years: breeding (25 May–15 Jul 1994–1995), fall migration (1 Sep–10 Oct 1994–1995), winter (1 Jan–15 Mar 1995–1996), and spring migration (15 Apr–20 May 1995–1996). Order of visits for each landscape was random both within a season and on a given day to minimize biases of survey date and time of day on patch size effects. Surveys were conducted from sunrise to 5 hrs after sunrise during spring-migratory and breeding seasons, and throughout the day (30 min after sunrise to 30 min before sunset) during fall-migratory and winter seasons. Counts were not conducted in heavy wind (>15 kph) or rain.

Statistical Analyses.—Presence of individual species was analyzed using binary logistic regression (Minitab 1998) for those species detected in ≥10 sites for each season individually (dependent variable). We used presence rather than abundance of bird species to avoid issues of long survey periods and multiple detections of the same birds (during single or multiple visits), both of which bias data toward smaller patches. A species was considered present if at least one individual was detected within a forest patch during at least one visit in a given season. Only individuals observed within a patch were included in analyses. Independent variables were forest-patch size class, physiographic section, year, and interactions between these variables. We grouped species into migratory, residency, microhabitat, and area dependency guilds (Table 1) based on patterns detected in other studies (e.g., Robbins et al. 1989) during the breeding season to generalize our results for discussion purposes only. Statistical analyses were considered significant at *alpha* level of 0.05.

RESULTS

Breeding Season.—We observed 39 bird species in the more fragmented landscape (Great Valley Section) and 42 species in the less fragmented landscape (Appalachian Mountain Section) during the 1994 breeding season, and 51 species in the more fragmented landscape and 56 species in the less fragmented landscape during the 1995 breeding season. Fourteen of 40 species were affected significantly by patch size (Table 1). One species, the Song Sparrow (scientific names of bird species are in Table 1), showed a significant negative response to patch size, whereas 13 species were positively associated with patch size. Nine species showed significant responses to landscape fragmentation. Blue Jay, Gray Catbird, Song Sparrow, Baltimore Oriole, and Common Grackle were detected more often in the more fragmented landscape, whereas Eastern Bluebird, Ovenbird, Red-eyed Vireo, and Scarlet Tanager were detected more frequently in the less fragmented landscape.

Fall-migratory Season.—Bird species richness for all forest patches combined was 35 in the less fragmented landscape and 39 in the more fragmented landscape in 1994, and 63 in the less fragmented landscape and 68 in the more fragmented landscape in 1995. Of the 28 species analyzed during fall migration, only six (Hairy Woodpecker, Pileated Woodpecker, Blue Jay, Black-capped/Carolina Chickadee, Tufted Titmouse, Brown Creeper), all permanent residents, showed significantly positive associations with patch size (Table 1). Conversely, the American Goldfinch was affected negatively. We observed seven species (White-breasted Nuthatch, American Robin, Gray Catbird, Magnolia Warbler, Yellow-rumped Warbler, Eastern Towhee, and White-throated Sparrow) more frequently in the more fragmented landscape and only one species (American Crow) more frequently in the less fragmented landscape.

Winter Season.—We observed 31 bird species during winter in the more fragmented landscape and 35 species in the less fragmented landscape in 1994–1995, and 36 species in the more fragmented landscape and 34 species in the less fragmented landscape in 1995–1996. Five of 25 wintering species (Red-bellied Woodpecker, Pileated Woodpecker, Eastern Phoebe, American Crow, White-breasted Nuthatch) responded positively to patch size, whereas only the Song Sparrow and Common Grackle responded negatively during winter (Table 1). Brown Creeper (interior specialist) and Dark-eyed Junco (edge-interior generalist) were detected more often in the less fragmented landscape; Red-bellied Woodpecker, Yellow-bellied Sapsucker, Northern Flicker, Eastern Phoebe, American Crow, American Robin, European Starling, Song Sparrow, and Common Grackle, all of which are classified as either edge specialists or edge-interior generalists, were observed significantly more often in the more fragmented landscape.

Spring-migratory Season.—We observed 71 bird species in the less fragmented landscape and 75 species in the more fragmented landscape during 1995, and 85 species in both landscapes during 1996. Of the 58 species that we analyzed, 24 were affected positively by patch size during spring migration and only five species (Gray Catbird, European Starling, Song Sparrow, Common Grackle, and Red-winged Blackbird) were negatively correlated with patch size (Table 1). Most species responding positively to patch size were long-distance migrants ($n = 16$); six permanent residents (Red-bellied Woodpecker, Pileated Woodpecker, American Crow, Fish Crow, Black-capped/Carolina Chickadee, and Tufted Titmouse) and two short-distance migrants (Blue-gray Gnatcatcher and Blue-headed Vireo) also were influenced positively by patch size. In contrast, species responding negatively to patch size were short-distance migrants or permanent residents and were edge specialists. Sixteen of 58 species responded significantly to fragmentation during spring migration; 10 species occurred more often in the more fragmented landscape. With the exception of American Redstart, these species were edge-interior generalists or edge specialists and not area sensitive. In contrast, Acadian

TABLE 1. Effects of patch size and landscape fragmentation on presence of individual bird species during breeding, fall-migratory, winter, and spring-migratory seasons in south-central Pennsylvania, 1994–1996. Species more likely ($P < 0.05$) to be detected in larger forest patches are noted by size+, in smaller patches by size−, in the more fragmented landscape (Great Valley Section) by frag+, and in the less fragmented landscape (Appalachian Mountain Section) by frag−. Species not significantly associated with either factor are noted by NS. An empty cell indicates a species was not analyzed during a given season due to limited observations (< 10 sites for both years combined).

	Guild[b]			Season			
Species[a]	R	MH	AD	Breeding	Fall migration	Winter	Spring migration
Permanent Residents							
Red-bellied Woodpecker (*Melanerpes carolinus*)	RES	EI	D	NS	NS	size+ frag+	size+
Hairy Woodpecker (*Picoides villosus*)	RES	I	D		size+	NS	NS
Pileated Woodpecker (*Dryocopus pileatus*)	RES	I	D		size+	size+	size+
Blue Jay (*Cyanocitta cristata*)	RES	EI	I	size+ frag+	size+	NS	frag+
American Crow (*Corvus brachyrhynchos*)	RES	E	I	NS	frag−	size + frag+	size+
Fish Crow (*C. ossifragus*)	RES	E	I	NS			size+, frag−
Black-capped (*Poecile atricapillus*)/Carolina (*P. carolinensis*) Chickadee[c]	RES	EI	I	size+	size+	NS	size+
Tufted Titmouse (*Baeolophus bicolor*)	RES	EI	D	size+	size+	NS	size+
White-breasted Nuthatch (*Sitta carolinensis*)	RES	I	I	NS	frag+	size+	NS
Brown Creeper (*Certhia americana*)	RES	I	D		size+	frag−	
Eastern Bluebird (*Sialia sialis*)	RES	E	I	frag−		NS	frag−
European Starling (*Sturnus vulgaris*)	RES	E	I	NS		frag+	size−
Song Sparrow (*Melospiza melodia*)	RES	E	I	size− frag+	NS	size− frag+	size− frag+
American Goldfinch (*Carduelis tristis*)	RES	E	I	NS	size−	NS	NS
Short-distance Migrants							
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	WIN	EI	I			frag+	
Northern Flicker (*Colaptes auratus*)	SUM	EI	I	NS	NS	frag+	frag+
Eastern Phoebe (*Sayornis phoebe*)	SUM	EI	I	NS	NS	size+ frag+	NS
Blue-headed Vireo (*Vireo solitarius*)	MIG	I	I		NS		size+
House Wren (*Troglodytes aedon*)	SUM	E	I	NS			frag+
Blue-gray Gnatcatcher (*Polioptila caerulea*)	SUM	EI	D	size+			size+

TABLE 1. Continued.

	Guild[b]			Season			
Species[a]	R	MH	AD	Breeding	Fall migration	Winter	Spring migration
American Robin (*Turdus migratorius*)	SUM	E	I	NS	frag+	frag+	NS
Gray Catbird (*Dumetella carolinensis*)	SUM	EI	I	frag+	frag+		size− frag+
Brown Thrasher (*Toxostoma rufum*)	SUM	E	I				frag+
Yellow-rumped Warbler (*Dendroica coronata*)	MIG	EI	I		frag+		NS
Common Yellowthroat (*Geothlypis trichas*)	SUM	EI	I	NS			frag+
Eastern Towhee (*Pipilo erythrophthalmus*)	SUM	EI	I	size+	frag+		frag+
Chipping Sparrow (*Spizella passerina*)	SUM	E	I	NS			frag−
White-throated Sparrow (*Zonotrichia albicollis*)	WIN	E	I		frag+	NS	frag+
Dark-eyed Junco (*Junco hyemalis*)	WIN	EI	I			frag−	
Common Grackle (*Quiscalus quiscula*)	SUM	E	I	frag+		size− frag+	size−
Red-winged Blackbird (*Agelaius phoeniceus*)	SUM	E	I				size−
Long-distance Migrants							
Yellow-billed Cuckoo (*Coccyzus americana*)	SUM	EI	I	size+			
Eastern Wood-pewee (*Contopus virens*)	SUM	EI	I	size+	NS		size+
Acadian Flycatcher (*Empidonax virescens*)	SUM	I	D	size+			size+ frag−
Great Crested Flycatcher (*Myiarchus crinitus*)	SUM	EI	D	NS			size+
Red-eyed Vireo (*Vireo olivaceus*)	SUM	EI	D	size+ frag−	NS		size+
Wood Thrush (*Hylocichla mustelina*)	SUM	EI	D	size+			size +
Blue-winged Warbler (*Vermivora pinus*)	SUM	E	I				size+
Northern Parula (*Parula americana*)	SUM	EI	I				size+
Magnolia Warbler (*Dendroica magnolia*)	MIG	I	I		frag+		size+
Black-throated Blue Warbler (*D. caerulescens*)	MIG	I	D		NS		size+
Black-throated Green Warbler (*D. virens*)	MIG	I	D		NS		size+
Black-and-white Warbler (*Mniotilta varia*)	SUM	I	D				size+
American Redstart (*Setophaga ruticilla*)	SUM	I	D				size+ frag+
Worm-eating Warbler (*Helmitheros vermivorum*)	SUM	I	D	size+			size+ frag−

TABLE 1. Continued.

Species[a]	Guild[b]			Season			
	R	MH	AD	Breeding	Fall migration	Winter	Spring migration
Ovenbird (*Seiurus aurocapilla*)	SUM	I	D	size+ frag−			size+ frag−
Scarlet Tanager (*Piranga olivacea*)	SUM	I	D	size+ frag−			size+
Indigo Bunting (*Passerina cyanea*)	SUM	E	I	NS			size+
Baltimore Oriole (*Icterus galbula*)	SUM	E	I	frag+			NS

[a] Species with distributions not significantly different based on size or fragmentation during all seasons (B = breeding, F = fall migration, W = winter, and S = spring) in which they were analyzed include: Mourning Dove (*Zenaida macroura*) (BW), Downy Woodpecker (*Picoides pubescens*) (BFWS), Carolina Wren (*Thryothorus ludovicianus*) (BS), Golden-crowned Kinglet (*Regulus satrapa*) (FW), Cedar Waxwing (*Bombycilla cedrorum*) (FS), Yellow Warbler (*Dendroica petechia*) (S), Chestnut-sided Warbler (S), Blackburnian Warbler (S), Bay-breasted Warbler (S), Blackpoll Warbler (S), Field Sparrow (*Spizella pusilla*) (BS), Northern Cardinal (*Cardinalis cardinalis*) (BFWS), Rose-breasted Grosbeak (*Pheucticus ludovicianus*) (S), Brown-headed Cowbird (*Molothrus ater*) (BS), and House Finch (*Carpodacus mexicanus*) (BW).

[b] Residency guilds (R) are year-round resident (RES), summer resident (SUM), winter resident (WIN), and migratory transient (MIG). Macrohabitats (MH) are interior-forest specialists (I), edge-interior generalists (EI), and edge specialists (E). Species (AD) were classified as area dependent (D) or area independent (I). Guilds are based on breeding season patterns exhibited by each species and are from: Whitcomb et al. (1981); Blake (1983, 1991); LaGory et al. (1984); DeGraaf et al. (1985); Andrle and Carroll (1988); Ehrlich et al. (1988); Martin (1988); Brooks and Croonquist (1990); Brewer et al. (1991); Brauning (1992); and O'Connell (1999).

[c] Treated as one species because ranges do not significantly overlap.

Flycatcher, Worm-eating Warbler, and Ovenbird, species typically requiring large patches of contiguous habitat, responded negatively to landscape-level fragmentation.

DISCUSSION

Our research suggests that responses to patch size and landscape fragmentation by bird species may not be consistent among seasons and requires a species-by-species analysis. Therefore, research on habitat use and distributional patterns at a landscape scale should include multiple seasons, particularly migration, rather than focusing only on a single season (Mehlman et al. 2005). For example, Blake (1986) reported a strong area effect during migration, but noted that birds may use small patches at least temporarily as they migrate through highly disturbed habitats. Specifically, interior-forest species, such as the Ovenbird, were found in smaller patches during migration than typically used during the breeding season (Blake and Karr 1984, 1987). In contrast, Somershoe and Chandler (2004) detected greater richness, more individuals, and greater individual abundance of most migrants in larger oak hammocks; however, their study sites were small (<3.1 ha) relative to those studied by Blake (1986) and Blake and Karr (1984, 1987).

Only the Pileated Woodpecker, an area-sensitive permanent resident, consistently was affected positively by patch size during each season analyzed. Black-capped/Carolina Chickadee and Tufted Titmouse were affected positively during all seasons except for winter. In contrast, the Song Sparrow was more likely to be found in small patches and in the more fragmented landscape during all seasons except fall migration. The only species consistently affected by fragmentation each season was the Gray Catbird, more commonly found in the more fragmented landscape. Relative amounts of edge habitat may influence the presence of both Song Sparrow (Arcese et al. 2002) and Gray Catbird (Cimprich and Moore 1995) and may lead to greater occurrences in the more fragmented landscape.

No long-distance migrants that breed within the study area (e.g., Eastern Wood-pewee, Red-eyed Vireo) showed a consistent pattern among the three seasons during which they were present (fall migration, spring migration, and breeding season). However, most maintained the same pattern between spring-migratory and breeding seasons. Transient species that breed far (>50 km) from the study areas (e.g., Blackpoll Warbler [*Dendroica striata*], Bay-breasted Warbler [*D. castanea*]) were not influenced by patch size, even including transients classified as area-dependent or interior-forest specialists (e.g., Blackburnian Warbler

[*D. fusca*]). In contrast, transients that breed near (within 30 km) the study area (e.g., Black-throated Blue Warbler, Black-throated Green Warbler) typically responded to patch size during spring migration. This apparent pattern of habitat use during spring migration warrants continued research as it provides possible evidence that birds shift preferred macro-habitats as they approach potential nesting sites. Rodewald and Brittingham (2002) found that most transient species (e.g., Philadelphia Vireo [*Vireo philadelphicus*], Blackpoll warbler) did not use habitats preferentially during fall migration in Pennsylvania, even though many locally-nesting migrants (e.g., Chestnut-sided Warbler [*Dendroica pensylvanica*], Black-throated Green Warbler) demonstrated non-random habitat use. Rodewald and Brittingham (2004) noted that most species in five wooded habitat types broadened their habitat use patterns during fall compared to habitat use during other seasons.

The greater likelihood of encountering short-distance migrants (e.g., Northern Flicker, American Robin, Gray Catbird, Eastern Towhee, Common Grackle) in the more fragmented landscape than in the less fragmented landscape may be due to relatively greater amounts of edge in the more fragmented landscape (Forman and Godron 1986). In contrast, most permanent residents (e.g., Hairy Woodpecker, Pileated Woodpecker, Tufted Titmouse) and long-distance migrants (e.g., Acadian Flycatcher, Red-eyed Vireo, Wood Thrush, Black-throated Blue Warbler, Worm-eating Warbler, Ovenbird, Scarlet Tanager), which exhibited an area effect in our study, are primarily interior-forest specialists or area-dependent species. Species found more commonly in the less fragmented landscape typically are classified as forest-interior or area-dependent species (e.g., Acadian Flycatcher, Red-eyed Vireo, Brown Creeper, Worm-eating Warbler). Graber and Graber (1983) found that amount of regional forest cover influences species during migration based on available food resources. Their results suggest that in our study, forest-interior species could respond to total amount of forest cover in the less fragmented landscape at a regional level. Our study illustrates that many species respond to broader scales during migration than may have been considered in previous migratory studies.

Continued research on the effects of forest fragmentation is important to document the seasonal value of forest patches to birds, particularly with continued habitat loss and fragmentation through residential and agricultural development. Preservation of large forest patches in the eastern deciduous forest is critical to provide necessary breeding habitat for declining populations of long-distance migrants (Yahner 2003). More research also must be conducted during other seasons at wintering sites and stopover points during migration to identify their role in the long-term survivorship of migratory birds (Mehlman et al. 2005).

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FRUIT QUALITY AND CONSUMPTION BY SONGBIRDS DURING AUTUMN MIGRATION

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ABSTRACT.—Seasonal fruits are an important food resource for small songbirds during autumn migration in southern New England. Therefore, conservation and management of important stopover sites used by migrating birds requires knowledge about nutritional requirements of songbirds and nutritional composition of commonly consumed fruits. We measured nutrient composition and energy density of nine common fruits on Block Island, Rhode Island, and conducted a field experiment to estimate consumption rates of three of these fruits by birds during autumn migration. Most common fruits on Block Island contained primarily carbohydrates (41.3–91.2% dry weight), and little protein (2.6–8.6%) and fat (0.9–3.7%), although three contained more fat: *Myrica pennsylvanica* (50.3%), *Viburnum dentatum* (41.3%), and *Parthenocissus quinquefolia* (23.6%). Bird consumption of high-fat, high-energy *V. dentatum* fruit and high-carbohydrate, low-energy *Phytolacca americana* fruit was greater than consumption of *Aronia melanocarpa*, a high-carbohydrate, low-energy fruit. We estimated that migratory birds on Block Island must eat up to four times their body mass in fruit wet weight each day to satisfy their energy requirements when eating low-energy fruits such as *P. americana*, and they cannot satisfy their protein requirements when eating only certain high-energy fruits such as *V. dentatum*. Our results suggest that many migratory birds must eat both fruits and insects to meet their dietary needs. Thus, shrubland habitat at important migratory stopover sites such as Block Island should be managed so that it contains a variety of preferred fruit-bearing shrubs and an adequate abundance of insects. *Received 30 May 2006. Accepted 24 September 2006.*

Many species of migratory songbirds that are primarily insectivorous during the breeding season consume large amounts of fruit during autumn migration (Thompson and Willson 1979, Herrera 1984, Parrish 1997), even though many common fruits may contain less protein and fat than is likely needed to fuel migratory flight (Berthold 1976, Herrera 1982, Bairlein and Gwinner 1994). The concentration of fat and carbohydrate in fruit varies considerably among plant species but the amount of protein in fruit is consistently low (Johnson et al. 1985, White 1989, Witmer 1996, Izhaki 1998). Given that birds must rebuild expended energy and protein stores at stopover sites during migration (Bauchinger and Biebach 1998, Piersma 2002), birds that eat fruits may satisfy their energy needs but have limited protein intake (Levey and Martínez del Rio 2001). The low protein content of fruits may explain why some birds are unable to maintain body mass when fed only fruit (Berthold 1976, Levey and Karasov 1989, Sedinger 1990, Izhaki 1992), although other characteristics of fruit pulp, such as secondary compounds or amino acid content, may also contribute to protein limitation (Parrish and Martin 1977, Izhaki and Safriel 1989, Mack 1990). Facultative frugivores, such as omnivorous migrating songbirds, typically have higher protein requirements than more specialized frugivores and, therefore, may be protein limited when feeding exclusively on low-protein fruits (Robbins 1993, Witmer 1998, Tsahar et al. 2006). Lack of sufficient protein in the diet of migratory songbirds can hinder their ability to regain body mass and result in an increased amount of time refueling at stopover sites (Berthold 1976, Bairlein and Gwinner 1994, Pierce and McWilliams 2004).

The ability of a fruit to satisfy protein requirements of a bird depends in part on the ratio of energy to protein in the fruit. This is because birds usually eat to satisfy their energy requirements rather than particular nutrient requirements (Robbins 1993). Therefore,

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birds will eat less of a fruit with a high energy to protein ratio, thus ingesting less protein, compared to a fruit with a relatively low energy to protein ratio. We can make predictions about which fruits can satisfy a bird's protein requirements by measuring the ratio of energy to protein in fruits eaten by selected migratory songbirds, and estimating the protein requirements of these same birds (Bosque and Pacheco 2000). However, relatively few studies have investigated how nutritional requirements of migratory birds relate to nutritional composition of fruits available at temperate stopover sites (Sorenson 1984, Johnson et al. 1985, Witmer 1998).

Our objectives were to: (1) measure the nutrient composition and energy density of fruits from nine common plant species that are abundant in southern New England's maritime shrublands, (2) identify which fruits can satisfy the energy and protein requirements of migratory songbirds, (3) estimate the rate at which migratory birds consume fruits from three plant species that differ in nutrient composition and energy density, and (4) provide suggestions for management of coastal shrubland that would improve habitat quality at stopover sites such as Block Island, Rhode Island.

METHODS

Study Site.—We estimated fruit quality during September–November 2001 and bird consumption of wild fruits during October 2004 at Clay Head Preserve (~190 ha) on Block Island, Rhode Island (41° 10′ N, 71° 34′ W). This island is an important stopover site for migratory songbirds during autumn migration (Baird and Nisbet 1960, Able 1977, Parrish 1997, Reinert et al. 2002). The maritime shrub community nearest the coast is dominated by stands of short northern bayberry (*Myrica pennsylvanica*) intermixed with *Rubus* spp. and poison ivy (*Toxicodendron radicans*). The more inland maritime shrub community consists of tall *M. pennsylvanica* mixed with northern arrowwood viburnum (*Viburnum dentatum*), black chokeberry (*Aronia melanocarpa*), shadbush (*Amelanchier* spp.), winterberry (*Ilex verticillata*), wild rose (*Rosa* spp.), and *Rubus* spp. Pokeweed (*Phytolacca americana*), a tall herbaceous plant, grows in scattered clumps in clearings and in the understory, and poison ivy and Virginia creeper (*Parthenocissus quinquefolia*) are found among the taller shrubs. Oriental bittersweet (*Celastrus orbiculatus*), autumn olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*) are common invasive species on Block Island.

Fruit Quality.—Fruit was collected on 4 days (9 Sep, 10 and 23 Oct, 3 Nov) during autumn 2001 within Clay Head Preserve. Species collected included *V. dentatum*, *A. melanocarpa*, *M. pennsylvanica*, *I. verticillata*, *P. quinquefolia*, *P. americana*, *C. orbiculatus*, wild rose hips, and *E. umbellata*. These are the most common fruits available to birds on Block Island during their autumn migration. Fruit samples were frozen in the field and stored frozen at −20° C at the University of Rhode Island until processed for nutrient composition. Processing in the laboratory involved thawing the fruits and then manually removing the seeds and stems. The seedless fruit was freeze-dried and ground in a small Waring blender.

Total energy content of fruit was measured by bomb calorimetry using a Parr 1266 Isoperibol Oxygen Bomb Calorimeter. Fat content was directly measured using a 2-g subsample of each fruit placed in separate ceramic thimbles (30 × 80 mm, medium porosity) and refluxed with petroleum ether for 6 hrs in a Soxhlet apparatus (Dobush et al. 1985). Nitrogen content was measured using a 3–4 mg sample of each fruit, which was then loaded and sealed into a clean tin capsule and placed in the autosampler of a Carlo-Erba NA 1500 Series II Elemental Analyzer attached to a continuous flow isotope ratio Micromass Optima Spectrometer (CF-IRMS). We estimated crude protein content by multiplying nitrogen content by 4.4 (Witmer 1998). Samples were then placed in a 550° C muffle furnace for ~3 hrs to obtain ash content. Total carbohydrate content was calculated as 100% minus percent fat, protein, and ash and included structural carbohydrates (e.g., plant fiber) and soluble carbohydrates (e.g., plant sugars). Mann-Whitney *U*-tests were used to compare fat and energy content of fruits picked in early (9 Sep, 10 Oct) versus late (23 Oct, 3 Nov) migration.

Nutrient Requirements.—We used published allometric equations to estimate energy and protein requirements of two bird species of different body mass that are common omnivorous fall migrants on Block Island: Hermit Thrush (*Catharus guttatus*) and Yellow-rumped Warbler (*Dendroica coronata*). Daily nitrogen requirement (DNR, mg N/day) of the Hermit Thrush was estimated using an equation for the Wood Thrush (*Hylocichla mustelina*): DNR = (911.2 mg N) × (body mass, kg)$^{-0.75}$/day (Witmer 1998). DNR of the Yellow-rumped Warbler was estimated using an allometric equation based on 10 species of omnivorous birds: DNR = (575.4 mg N) × (body mass, kg)$^{-0.76}$/day (Tsahar et al. 2006). We used this interspecific allometric equation because (a) there is no published single-species equation for a small migratory passerine with feeding habits similar to Yellow-rumped Warblers, and (b) this interspecific equation along with that for Wood Thrush provides a range of estimated nitrogen requirements that is useful for evaluating nutritional adequacy of fruits. Field metabolic rate (FMR, kJ/day) for free living, non-reproducing birds was estimated using: log FMR = 1.145 + (0.53 × log body mass, g) (Koteja 1991). Daily energy requirement (DER, kJ/day) was estimated using DER = FMR/0.64 assuming a 64% efficiency of conversion of dietary energy (Karasov 1990). Data on the observed diets of Hermit Thrushes and Yellow-rumped Warblers during autumn stopover on Block Island were available from earlier work (Parrish 1997).

We used estimated DER and the energy density of each fruit (kJ/g dry mass) to calculate dry food intake required to meet daily energy requirements. Wet food intake was then calculated based on the measured percent mass loss between wet fruit mass with seed and dry fruit mass without seed. We assumed 75% mass loss between wet with seed to dry without seed for *M. pennsylvanica* because this fruit contains waxy pulp. We plotted the percent protein required in fruit to meet daily protein requirements if birds ate sufficient fruit to satisfy their energy requirements. We then plotted measured protein and energy densities in wild fruits to identify which fruits would satisfy protein requirements of birds. We expanded our analysis of fruit quality in relation to protein requirements of birds beyond fruits for which we measured nutrient composition by including nutrient composition of other fruits present on Block Island that were published by White (1989).

Fruit Removal.—We randomly selected and marked one branch on five separate *V. dentatum*, *P. americana*, and *A. melanocarpa* plants within the inland maritime shrubland community on 9 Oct 2004. We selected a companion branch and enclosed the fruiting portion of this branch with translucent netting ensuring the netted branches were still exposed to environmental conditions while preventing birds from accessing the fruits. We counted the total number of fruits on each branch when it was initially selected and weekly thereafter for three weeks to estimate the rate of fruit removal and consumption at Clay Head Preserve during autumn migration. We recounted fruits on a given branch until we arrived at the same number of fruits at least twice to obtain an accurate measurement of the number of fruits on each branch. We counted separately the unripe fruits (defined as those fruits that were more than 50% green) and ripe fruits on each branch of *P. americana*.

We compared the initial number of fruits per branch among the three plant species with two-way ANOVA with species and branch type (enclosed, unenclosed) as grouping variables. We calculated the percent of fruits remaining each week on each enclosed (*V. dentatum*, $n = 5$; *P. americana*, $n = 4$; *A. melanocarpa* $n = 5$) and unenclosed (*V. dentatum*, $n = 5$; *P. americana*, $n = 4$; *A. melanocarpa* $n = 5$) branch to estimate changes in fruit numbers over time (Drummond 2005). The arcsine transformed values were analyzed using repeated measures ANOVA. We also developed a fruit consumption index by dividing the percent of fruits remaining on unenclosed branches by the percent of fruits remaining on companion enclosed branches (*V. dentatum*, $n = 5$; *P. americana*, $n = 3$; *A. melanocarpa*, $n = 5$). This ratio was subtracted from one to yield an index in which greater values reflect higher cumulative consumption over time. We used repeated measures ANOVA to analyze changes in the arcsine transformed fruit consumption index over time. Two pairs of *P. americana* branches were eliminated from the analysis because one branch in each pair died before the end of the study.

RESULTS

Fruit Quality.—Most fruits on Block Island contained primarily carbohydrates (41.3–91.2% dry weight) and little fat (0.9–3.7%; Table 1), except for *M. pennsylvanica*, *V. dentatum*, and *P. quinquefolia* which had appreciably higher fat content (50.3, 41.3, and 23.6%, respectively). These three higher-fat fruits had energy densities almost twice as great as other fruits such as *P. americana* and *E. umbellata* (Table 1). We found no significant seasonal change in energy density (U = 93, P = 0.82) or fat content (U = 118, P = 0.97) of fruits throughout the autumn period. We estimated that migratory birds must eat approximately three to four times their body mass in *P. americana* berries to satisfy their energy requirements (Table 2). In contrast, songbirds that eat *V. dentatum* fruit must eat less than or up to their own body mass in fruit each day because of its higher energy density (Table 2). If birds eat only enough to satisfy their energy requirements, we estimated that omnivorous birds such as Yellow-rumped Warblers could not satisfy their daily protein requirements by eating high-energy fruits like *M. pennsylvanica* and *V. dentatum* (Fig. 1). Many more fruits would not satisfy daily protein requirements if minimum nitrogen requirements were as high as those estimated for the Hermit Thrush. However, most birds would likely meet their daily protein requirements if feeding exclusively on lower energy fruits such as *P. americana*, although low-energy fruits with less protein such as *V. corymbosum* would likely be protein deficient (Fig. 1).

Fruit Removal.—When we first counted fruits on 9 October, *A. melanocarpa* had significantly more fruits per branch than both *V. dentatum* and *P. americana* (species: $F_{2,20}$ = 11.2, P = 0.001). There were no significant differences in number of fruits on enclosed and unenclosed branches on 9 October (branch type: $F_{1,20}$ = 2.7, P = 0.11; species × branch type: $F_{2,20}$ = 0.4, P = 0.68). The percent fruit remaining on unenclosed branches during the next 3 weeks decreased with *V. dentatum* losing the greatest percent of its fruit most rapidly (time: $F_{2,22}$ = 18.9, P < 0.001; species: $F_{2,11}$ = 17.9, P < 0.001; time × species: $F_{4,22}$ = 0.3, P = 0.86; Fig. 2). The per-

TABLE 1. Nutrient composition (% dry weight ± SE) and energy density (kJ/g dry weight ± SE) of common fruit species on Block Island, Rhode Island collected during September–November 2001. Numbers associated with each species are used to identify species in Fig. 1.

Species	Common name	Fat	Protein	Carbohydrate	Ash	Energy density
1 *Myrica pennsylvanica*	Bayberry	50.3 ± 1.4	3.0 ± 0.0	41.3 ± 0.2	3.4 ± 1.3	28.7 ± 0.5
2 *Viburnum dentatum*	Viburnum	41.3 ± 5.8	2.6 ± 0.0	50.0 ± 5.5	3.7 ± 1.0	27.4 ± 0.6
3 *P. quinquefolia*	Virginia creeper	23.6 ± 4.8	6.0 ± 0.0	67.7 ± 5.3	3.7 ± 0.4	22.3 ± 0.0
4 *Ilex verticillata*	Winterberry	3.7 ± 0.7	2.9 ± 0.0	88.1 ± 0.7	3.3 ± 0.3	19.9 ± 0.7
5 *Celastrus orbiculatus*	Bittersweet	2.6 ± 1.1	8.6 ± 0.1	89.1 ± 1.4	3.3 ± 0.5	18.8 ± 0.9
6 *Aronia melanocarpa*	Chokeberry	0.9 ± 0.6	3.5 ± 0.0	91.2 ± 0.8	2.9 ± 0.4	18.1 ± 0.6
7 *Rosa* spp.	Rose	2.2 ± 1.7	5.6 ± 0.0	87.5 ± 1.6	5.4 ± 0.2	17.3 ± 0.8
8 *Phytolacca americana*	Pokeweed	2.9 ± 0.1	5.8 ± 0.0	79.8 ± 0.5	12.4 ± 0.4	16.5 ± 1.0
9 *Elaeagnus umbellata*	Autumn olive	2.1 ± 0.2	6.0 ± 0.0	89.9 ± 0.7	3.0 ± 0.7	15.8 ± 0.3

TABLE 2. Estimated required fruit intake for two migratory bird species based on measured energy density of the fruits (Table 1) and predicted daily energy requirements of the birds[a].

		Dry food intake (g/day)		Wet food intake (g/day)	
Species	Common name	HETH	YRWA	HETH	YRWA
Myrica pennsylvanica	Bayberry	4.71	2.97	18.83	11.89
Viburnum dentatum	Viburnum	4.97	3.13	21.68	13.69
P. quinquefolia	Virginia creeper	6.04	3.81	34.04	21.49
Ilex verticillata	Winterberry	6.80	4.29	22.34	14.10
Celastrus orbiculatus	Bittersweet	7.20	4.55	66.07	41.71
Aronia melanocarpa	Chokeberry	7.39	4.66	25.87	16.33
Rosa spp.	Rose	7.65	4.83	35.72	22.55
Phytolacca americana	Pokeweed	8.06	5.09	90.71	57.26
Elaeagnus umbellata	Autumn olive	8.67	5.47	68.16	43.03

[a] Daily energy requirements were estimated using the average body mass of each species: Hermit Thrush = 31.2 g (HETH; Jones and Donovan 1996); Yellow-rumped Warbler = 13.1 g (YRWA; Hunt and Flaspohler 1998), an allometric equation: Log FMR = 1.145 + 0.53 log mass (g) (Koteja 1991), and assuming a 64% efficiency of conversion of dietary energy: DER = FMR/0.64 (Karasov 1990).

cent fruit remaining on enclosed branches also decreased over time (time: $F_{2,22} = 5.9$, $P = 0.009$) although at a much slower rate than it did on unenclosed branches (Fig. 2). Enclosed *A. melanocarpa* and *P. americana* branches lost a greater percent of their fruit than *V. dentatum* during the 3 weeks (species: $F_{2,11} = 5.5$, $P = 0.022$; time × species: $F_{4,22} = 0.5$, $P = 0.73$; Fig. 2). Rate of consumption was higher earlier in the season than later with consumption of *V. dentatum* fruit greater than consumption of either *P. americana* or *A. melanocarpa* fruit (time: $F_{2,20} = 11.4$, $P < 0.001$; species: $F_{2,10} = 35.3$, $P < 0.001$; time × species: $F_{2,10} = 1.7$, $P = 0.20$; Fig. 3).

DISCUSSION

Birds Eat Certain Fruits During Migration.—Our results show that fruits were readily consumed by birds during autumn migration although consumption rates differed by plant species. Fruit removal in excess of loss due to natural abscission can be attributed to bird consumption because birds are the most important vertebrate consumers of fruit on Block Island. There are only nine terrestrial mammal species on the island and none of these species eats primarily fruits (Lang and Comings 2001).

Birds on Block Island ate more high-energy *V. dentatum* fruit than the lower energy fruits of *P. americana* and *A. melanocarpa*. Parrish (1997) also found that *V. dentatum* was the most prevalent fruit in the diet of fall migrants on Block Island. *P. americana* and *M. pennsylvanica* were also readily consumed by birds, although consumption of *M. pennsylvanica* was almost exclusively by Yellow-rumped Warblers (Parrish 1997). This is most likely because the fat in this fruit is primarily composed of wax esters that can only be efficiently digested by a few species including the Yellow-rumped Warbler (Place and Stiles 1992). *V. dentatum* fruits are more energy dense because of their high fat content compared to the high-carbohydrate fruits *P. americana* and *A. melanocarpa*. Total carbohydrate content of fruits includes structural carbohydrates, such as cellulose, that most passerines cannot digest, and more readily digestible soluble carbohydrates, such as hexose sugars (Karasov 1990, Martínez del Rio and Karasov 1990). We were unable to ascertain if birds ate less high-carbohydrate fruits such as *A. melanocarpa* because the carbohydrate was mostly structural carbohydrates as we only measured total carbohydrates of fruits. Patterns of fruit consumption were also not simply related to dietary protein because *P. americana* had more protein than *V. dentatum* and most other fruits sampled in our study. These results suggest that fruit selection by birds on Block Island was not simply related to differences in macronutrient composition between fruits.

Many mechanisms have been proposed to explain the characteristics of fruits and other foods that birds may use to choose their diets. For example, studies of wild and captive songbirds have shown that some species preferentially select high-fat fruits (Stiles 1993, Fuentes 1994), or high-sugar fruits (Levey

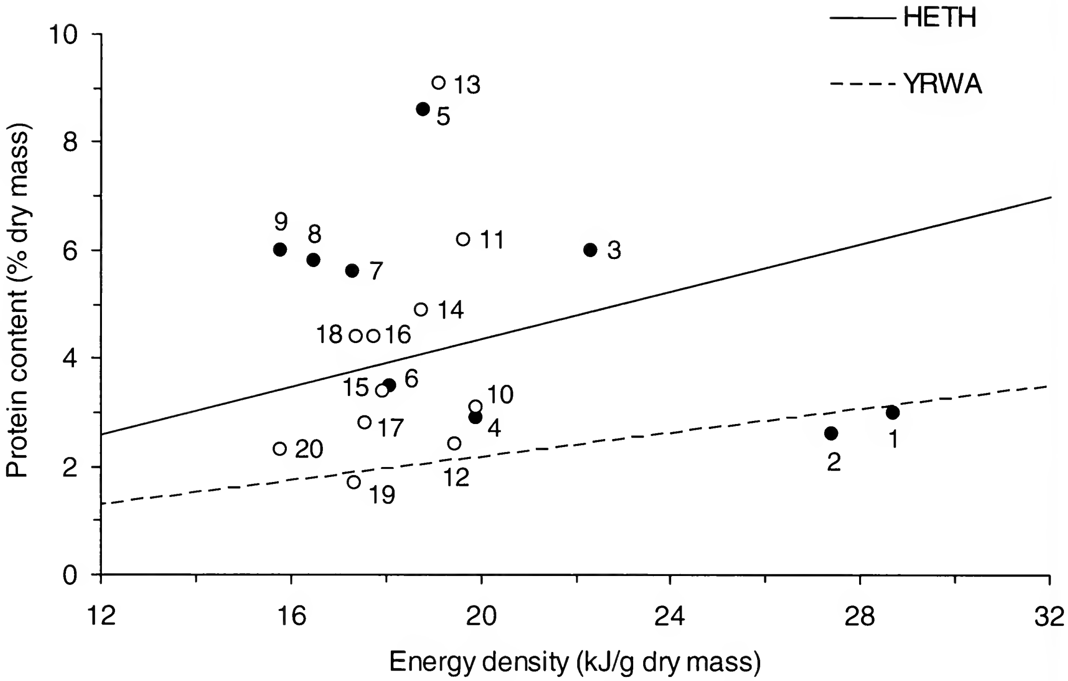

FIG. 1. Estimated dietary protein content required to meet the daily protein requirements for two representative migratory species: Hermit Thrush (HETH) and Yellow-rumped Warbler (YRWA). Energy density and protein content of 20 fruit species on Block Island are represented by circles; fruits below the lines do not contain sufficient protein to satisfy a bird's daily requirements. Solid circles denote fruiting plant species (Table 1). Open circles denote fruiting plant species for which nutrient composition was provided by White (1989): 10 = *Viburnum acerifolium*; 11 = *Smilax rotundifloria*; 12 = *Aronia prunifolia*; 13 = *Sambucus canadensis;* 14 = *Vitis labrusca*; 15 = *Prunus virginiana*; 16 = *Lonicera japonicum*; 17 = *Rosa virginiana*; 18 = *Aronia arbutifolia*; 19 = *Vaccinium corymbosum*; 20 = *Rubus occidentalis*.

1987, Lepczyk et al. 2000), or fruits with particular amino acids (Parrish and Martin 1977), fatty acids (McWilliams et al. 2002, Pierce et al. 2004), colors (Willson et al. 1990, Puckey et al. 1996), or certain pulp-to-seed ratios or seed size (Sorenson 1984, Izhaki 1992, Murray et al. 1993, Stanley and Lill 2002). Secondary compounds may also affect fruit choice because birds may eat a diversity of fruits to avoid toxic levels of particular secondary compounds (Barnea et al. 1993; Cipollini and Levey 1997a, 1997b; Levey and Cipollini 1998; Schaefer et al. 2003). Secondary compounds in fruits may also interfere with protein digestion, which may cause birds to switch to a diet of insects before resuming fruit consumption (Izhaki and Safriel 1989).

Fruit selection in free-living birds may also be related to ecological context (Baird 1980, Moermond and Denslow 1983, Sargent 1990, Whelan and Willson 1994). For example, *V. dentatum* is a high-energy, consumed fruit that is also one the most abundant fruiting species in the habitats used by songbirds during stopover on Block Island. In contrast, *P. americana* is a high-carbohydrate fruit that was consumed at a lower rate than *V. dentatum*, and is less abundant and more patchily distributed throughout the habitat. Thus, both ecological and nutritional factors likely interact to affect patterns of fruit consumption by birds during autumn migration.

Nutritional Adequacy of Fruits for Migrating Birds.—Fruits provide an easily accessible resource for birds that requires relatively little energy to acquire compared to foraging on aerial insects (Parrish 1997). In addition, fruit availability may be increasingly important as the autumn season progresses because insect resources become more unpredictable and scarce with decreasing temperatures and inclement weather conditions (Parrish 2000).

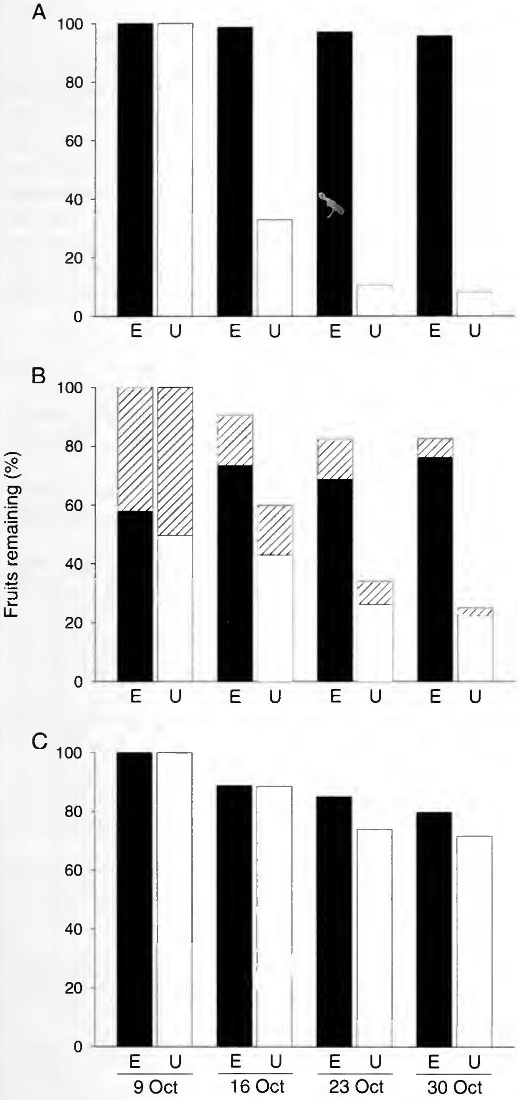

FIG. 2. Mean percent fruit remaining on enclosed (E) and unenclosed (U) branches for *V. dentatum* (A), *P. americana* (B), and *A. melanocarpa* (C). Fruit counts on Block Island were conducted on three sampling dates following initial fruit counts on 9 October 2004. Hatched bars on B denote unripe fruits on enclosed and unenclosed branches.

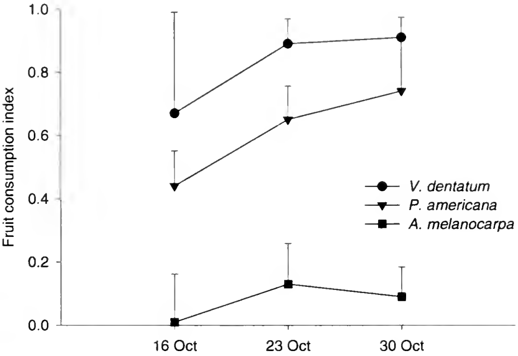

FIG. 3. Mean (± SD) fruit consumption index (1 − [% fruits remaining on unenclosed branches divided by % fruits remaining on companion enclosed branches]) for *V. dentatum*, *P. americana*, and *A. melanocarpa* on Block Island during October 2004. Fruits with index values closer to 1.0 had higher cumulative consumption over time.

We have shown that songbirds that consume only fruits may satisfy their energy requirements but may not satisfy their daily protein requirements because temperate fruits may have too little protein relative to energy content to meet their protein requirements (Witmer 1998). This protein limitation may be particularly difficult for songbirds during migration which must replenish some protein along with fat reserves (McWilliams et al. 2004). Studies with captive birds suggest they can maintain body weight when fed only fruit (Bairlein and Simons 1995, Bairlein 1996), although birds eating mixed fruit and insect diets usually gain mass more rapidly than birds eating either fruit or insects alone (Bairlein and Simons 1995, Parrish 2000). Diet switching or mixing may satisfy the bird's nutrient requirements but may also require time for digestive adaptation, which could increase time spent refueling and delay the overall speed of migration (McWilliams and Karasov 2005). Migratory birds at stopover sites such as Block Island probably must consume a variety of fruits with different energy and protein content, or consume some insects along with fruits to satisfy their protein and energy requirements as observed in some migrating birds (White and Stiles 1990, Parrish 1997). Further studies are needed that measure protein requirements of a variety of birds during migratory and non-migratory periods before we can more accurately predict whether certain fruits provide adequate energy and protein for a given bird species.

CONSERVATION IMPLICATIONS

Many populations of neotropical songbird migrants have declined over the past few decades (Askins et al. 1990). In the past, most emphasis has been placed on conservation of songbird populations in breeding and wintering areas. However, energetically demanding annual migrations can result in mortality rates 15 times higher than during breeding and wintering seasons (Sillett and Holmes 2002). Small songbirds require abundant food resources over the length of their migratory route to successfully complete migration. Thus, availability of suitable stopover habitat is critical for songbird survival and long-term conservation of these populations.

The east coast of the United States is an important migration corridor for many species of landbird migrants. The maritime shrubland habitats that serve as stopover sites receive large numbers of migrants, particularly in areas near significant barriers to migration such as large bodies of water. The superabundant fruits present at these sites are important food resources that are used extensively by migrating birds during autumn stopover. For example, migrant abundance is highest in habitats with greater fruit availability during autumn migration (Blake and Hoppes 1986, Martin and Karr 1986, Suthers et al. 2000, Rodewald and Brittingham 2004). Experimental removal of available fruits decreased local abundance of autumn migrants on Block Island (Parrish 2000) and birds overwintering in the southern United States (Borgmann et al. 2004). Thus, seasonally abundant fruits can be a significant food resource for migrating songbirds in temperate regions of eastern North America (White 1989, Parrish 1997).

Eastern shrubland habitats are becoming rare and more frequently disturbed as development increases (Moore et al. 1995, Askins 2000). In light of the importance of these habitats for migrating birds, the diversity of native fruiting plants in existing shrublands should be maintained to provide the resources needed for efficient migratory refueling. Managers and landowners should focus on creating suitable stopover habitat by cultivating or planting high-energy fruits such as *V. dentatum* along with lower energy, higher-protein fruits such as *P. americana* that are widely consumed by songbirds and that are native to the northeastern United States. More specific management recommendations require additional research and a more comprehensive analysis of fruit consumption across a broader range of habitats and temperate fruit species.

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INVASIVE FRUITS, NOVEL FOODS, AND CHOICE: AN INVESTIGATION OF EUROPEAN STARLING AND AMERICAN ROBIN FRUGIVORY

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ABSTRACT.—We compared the feeding choices of an invasive frugivore, the European Starling (*Sturnus vulgaris*), with those of a native, the American Robin (*Turdus migratorius*). Using captive birds, we tested whether these species differ in their preferences when offered a choice between a native and an invasive fruit, and between a novel and a familiar food. We examined willingness to eat fruits of selected invasive plants and to select a novel food by measuring the time elapsed before feeding began. Both species demonstrated significant preferences for invasive fruits over similar native fruits in two of three choice tests. Both starlings and robins ate autumn olive (*Elaeagnus umbellata*) fruits significantly more willingly than Asiatic bittersweet (*Celastrus orbiculatus*). Starlings, but not robins when choosing between a novel and a familiar food, strongly preferred the familiar food. We found no differences in willingness of birds to eat a novel food when it was the only food available. These results suggest that some fleshy-fruited invasive plants may receive more dispersal services than native plants with similar fruits, and that different frugivores may be seed dispersers for different invasive plants.

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Seed dispersal by birds is a widespread mutualism existing in many habitats and involving many species (Willson 1990). Typically, each fleshy-fruited plant and each fruit-eater interacts with several counterparts during the course of a year forming a loosely networked assemblage of participants. While the diffuse coevolution of these systems has protected them from disruption due to species losses in the past (Janzen 1983), it also provides a point of entry for newly arrived participants. Many habitats now support both introduced fleshy-fruited plants and introduced frugivores creating the potential for non-native species to promote each other's populations (Simberloff and Von Holle 1999, Richardson et al. 2000).

There are several reasons to be particularly concerned about the addition of non-native species to avian-mediated seed-dispersal systems. First, birds probably disperse more seeds than any other vertebrate group (Stiles 2000). Plants with bird-dispersed seeds use similar signals to attract dispersers worldwide. Fruits are small, red to black in color, and lack pulp protection (e.g., Gautier-Hion et al. 1985, Wheelwright and Janson 1985), but may contain secondary plant compounds (Cipollini and Levey 1997). The conservative nature of these characteristics may promote the formation of new plant/disperser relationships when fleshy-fruited plants or frugivorous birds spread to new ranges. Second, plants with bright, bird-attracting fruits are often favored by horticulturalists and, thus, especially prone to introduction (Stiles 1982, Mack 2000, Reichard et al. 2001). Finally, plants may benefit from rapid range expansion (Debussche et al. 1982, Moody and Mack 1988, Cronk and Fuller 1995) as a result of the wide-ranging habits of many birds. If seed dispersers prefer fruits of introduced plants to those of natives (LaFleur 2006), native fleshy-fruited plants may be out-competed for dispersal services (Bass 1990, Sallabanks 1992).

Frugivore behavior may also affect the acceptance of new fruits into seed-dispersal systems. Birds vary in flexibility of their foraging behavior (Greenberg 1983, 1984; Webster and Lefebvre 2001), which can be measured by the extent of avoidance, or neophobia, an animal exhibits when confronted with a novel food or situation (Greenberg 1983, 1989, 1990; Webster and Lefebvre 2001). Neophobia varies among bird species (e.g., Greenberg 1984, 1989; Mettke-Hofmann et al. 2002) and may regulate the incorporation of new foods into the diet (Webster and Lefebvre 2001).

We examined the foraging behavior of frugivorous birds in relation to fleshy-fruited invasive plants. We compared feeding choices by an invasive bird, the European Starling

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(*Sturnus vulgaris*), with those of a native bird, the American Robin (*Turdus migratorius*). Starlings and robins are appropriate for comparison as gape size (White 1989), body mass, and energy requirements (Taitt 1973, Hazelton and Robel 1984) are similar. In addition, neither starlings (Martínez del Rio et al. 1988), nor robins (Karasov and Levey 1990) are able to digest sucrose. Both are abundant, wide-ranging, and have diets that vary seasonally to include fruits (Lindsey 1939, Fischl and Caccamise 1986, Wheelwright 1986). Further, both are known to forage in old-field habitat, agricultural settings, and human-impacted areas where introduced plants often occur. Both starlings and robins have the potential to be highly effective seed dispersers for plants whose fruits they prefer because of their widespread ranges and large numbers.

We examined whether European Starlings and American Robins differed in their (1) preference when offered a native and an invasive fruit, (2) willingness to eat selected invasive fruits when no other fruit was present, and (3) willingness to test a novel food in two situations: when a familiar food was also present and when it was absent. We predicted similarities in digestive physiology and energy requirements would cause starlings and robins to make similar choices when selecting between native and invasive fruits matched as closely as possible for morphology and phenology in old-field habitat. We also expected that when no other food was available, starlings and robins would demonstrate similar preferences for invasive fruits. When examining the willingness of starlings and robins to test a novel food in the presence of a familiar food, we predicted that both species would select the familiar food, a known source of nutrition. We predicted that starlings, an extremely successful invasive bird, would test a novel food more quickly than robins when it was the only food available.

METHODS

Bird Capture and Maintenance.—We captured starlings (seven males, four females) with mist nets and walk-in traps during winter 2000–2001 in Mansfield and Chaplin, Connecticut. We captured robins (two males, six females) with mist nets in April 2002 in Mansfield and Willington, Connecticut. All birds were housed in single species groups of two to four in indoor aviaries (1.65 × 1.65 × 2.44 m) at the University of Connecticut's Avian Research Facility in Storrs, Connecticut. We maintained birds under dark: light conditions that replicated natural photoperiod; lighting was provided by a large window supplemented with fluorescent lights. Birds were held at 21° C during June-September and 10° C during November–April to mimic natural seasonal temperature changes. Temperatures were gradually decreased or increased in October and May, respectively. We provided birds with a diet of mashed bananas and soy protein *ad libitum* (Denslow et al. 1987) between tests to maintain them in a fruit-ready state of digestive physiology. All birds were allowed to acclimate to captivity for at least 14 days before participating in experiments. All work was conducted under proper state and federal permits with approval of the Institutional Animal Care and Use Committee at the University of Connecticut.

Selection and Collection of Fruits.—Fleshy-fruited woody plants are an important component of the invasive flora of the northeastern United States. Nearly all of the invasive shrubs and vines in this region have seeds thought to be bird dispersed (Silander and Klepeis 1999). We focused on three of the most aggressive of these: autumn olive (*Elaeagnus umbellata*), Asiatic bittersweet (*Celastrus orbiculatus*), and multiflora rose (*Rosa multiflora*) (Silander and Klepeis 1999). No native plants with fruit morphology or phenology comparable to Asiatic bittersweet were locally available and we omitted bittersweet from our choice tests and instead included glossy buckthorn (*Frangula alnus*). Glossy buckthorn is also an aggressive woody invasive, which is widely distributed in the northeastern states. In latency tests, we used autumn olive, Asiatic bittersweet, and multiflora rose.

We offered birds three combinations of a native and an invasive plant's fruit (Table 1) in choice tests matched as closely as possible on the basis of morphological similarity, fruiting times, and co-occurrence in local old-field habitat. Autumn olive, winterberry (*Ilex verticillata*), highbush blueberry (*Vaccinium corymbosum*), and glossy buckthorn all produce round, berry-like fruits having one or more

TABLE 1. Characteristics of fruits of invasive and native plants used in this study. Means and sample sizes for fruit mass, seed mass, and pulp:seed ratio are for fresh, locally collected fruits, except as noted. Previously published studies were consulted for energy and chemical component data for dry pulp.

Species	Pair	Color	*n*	Fruit mass (mg)	Seed mass (mg)	Pulp:seed ratio	KJ/g	Lipids (%)	Soluble carbohydrates (%)	Protein (%)	Region of origin
Autumn olive	1	red	20	304.5	33.0	8.63	17.34^{a}	1.4^{a}	62.7^{a}	4.7^{a}	Eurasia^{e}
Winterberry	1	bright red	20	96.0	31.0	2.10	18.40^{a}	4.3^{a}	43.1^{a}	2.6^{a}	Native^{e}
Multiflora rose	2	brick red	10	106.0	38.0	2.04	17.52^{a}	1.5^{a}	55.1^{a}	7.6^{a}	East Asia^{e}
Swamp rose	2	brick red	10	327.0	53.0	5.17	17.56^{a,b}	1.1^{a,b}	39.6^{a,b}	2.8^{a,b}	Native^{e}
Glossy buckthorn	3	blue/black	20	301.0	98.0	2.33	18.18^{a,d}	2.8^{c}	45.3^{c}	6.5^{c}	Eurasia^{e}
Highbush blueberry	3	blue/black	20	140.5	0.9^{a}	471.8^{a}	17.33^{a}	0.8^{a}	85.5^{a}	1.7^{a}	Native^{e}
Asiatic bittersweet		orange	20	173.0	54.5	2.29	19.96^{a}	1.7^{a}	56.8^{a}	10.4^{a}	East Asia^{e}

[a] White (1989).
[b] Data for swamp rose unavailable; data for *R. virginiana* were substituted.
[c] Hampe and Bairlein (2000).
[d] Data for glossy buckthorn unavailable; data for common buckthorn (*Rhamnus catharica*) were substituted.
[e] Gleason and Cronquist (1991).

seeds. The fruits of both multiflora and swamp rose (*Rosa palustris*) are typical rose hips. Temperate bird-dispersed fruits vary widely in many characteristics (White 1989) and we selected carbohydrate-rich fruits with masses under 350 mg.

Autumn olive, winterberry, and multiflora rose fruits were collected in Storrs, Connecticut; swamp rose in Eastford, Connecticut; and glossy buckthorn and highbush blueberry in Putnam, Connecticut. In all cases (except multiflora rose and swamp rose), fruit combinations to be tested together were picked at the same site and on the same day. Perishable fruits, typically removed from plants by birds before severe fall frosts, or fruits paired with such species (glossy buckthorn, highbush blueberry, autumn olive, and winterberry) were collected and refrigerated the evening prior to, or the morning of use. Roses produce persistent fruits that remain on plants throughout the winter. Rose fruits were collected, placed in sealed containers, and frozen until use to ensure an adequate supply. We collected rose fruits in late October 2001 for starlings and early November 2002 for robins. We did not include Asiatic bittersweet in these tests as there was no local supply of American bittersweet (*Celastrus scandens*) or other appropriate native fruit with which to pair it.

We used the fruits of three invasive species in the latency tests: autumn olive, Asiatic bittersweet, and multiflora rose. We collected autumn olive fruits for latency tests the evening before, or the morning of experiments. Asiatic bittersweet and multiflora rose fruits used in latency tests were collected in late December 2002, and frozen until use to ensure an adequate supply of unspoiled fruits. We collected all fruits for these trials in Storrs, Connecticut.

Both choice and latency trials were conducted when fruit was available to wild birds; thus, trials were spread over the course of late summer through winter. We conducted choice tests with glossy buckthorn and highbush blueberry in late July and August 2002, autumn olive and winterberry in October 2002, and multiflora rose and swamp rose in January 2002 (starlings) and December 2002 (robins). We conducted latency tests with autumn olive during September and October 2002, and with Asiatic bittersweet and multiflora rose from January to early March 2003.

Choice Tests with Native and Invasive Fruits.—We used choice tests to examine whether starlings and robins differed in their preferences when allowed to select between a native and an invasive fruit. We offered birds equal numbers of fruits of the combination to be tested the day prior to choice tests. We then removed any remaining fruits after checking to ensure that birds had eaten some of both food choices, and held birds overnight without food to standardize motivation to feed during the trial. We conducted all choice tests in an aviary (1.75 × 1.50 × 2.40 m) that prevented visual contact between the experimental bird and other birds. Perches were placed along the back wall of the aviary and a large stainless steel water bowl (19 cm diameter) was placed on the floor in the center of the aviary. The aviary floor was marked with two 19-cm circles to the left and right of, and immediately adjacent to the water bowl. Fruits of the combination to be tested were placed in these circles prior to introducing a bird into the aviary. Placement of the invasive fruit was randomized by a coin-toss for each fruit pair and each bird (= trial). Equal numbers and masses (to the nearest 0.1 g) of the fruits to be tested for each trial were placed in the appropriate circles. Five fruits of each species were offered in the autumn olive/winterberry trials; variation in fruit masses among trials ranged from 1.0 to 1.3 g per species. We also offered birds five fruits in the glossy buckthorn/highbush blueberry trials with matched masses among trials ranging from 0.9 to 1.5 g per species. We used only three fruits each (to minimize the weight disparity between these two species) in the swamp rose/multiflora rose trials. Fruit masses were matched to the nearest 0.1 g and ranged from 0.5 to 0.8 g. We tested food placement positions with maintenance diet prior to performing any choice tests to ensure that birds showed no bias toward the left or right position. Neither individuals nor species showed any such bias (NEL, unpubl. data).

After we set the fruits in place, we covered both the fruits and the filled water bowl with see-through cloth mesh, and released the bird to be tested into the aviary. Each bird was allowed a 5-min inspection period to become familiar with the experimental chamber and to inspect the fruit choices. We removed the mesh covering at the end of 5 min by pulling it through an opening that extended along the base of the aviary, and observed bird behavior from a blind. We scored each fruit eaten as a choice. Trials ended when 1 hr had elapsed since the end of the inspection period, or when all of one type of fruit had been consumed. We totaled the numbers of fruits eaten per plant species at the end of each trial. The plant species with the most fruits consumed was considered preferred. If a bird showed no interest in eating within the first 20 min, the trial was terminated and the test was conducted later in the day or at a later date. Each bird was tested only once with each combination of fruits. All trials began between 0730 and 1200 hrs EST.

Latency Tests with Invasive Fruits.—We compared the willingness of starlings and robins to eat fruits of selected invasive plants when no other food was available using latency tests. Tests were conducted in small cages (0.65 × 0.65 × 0.65 m) in which birds were prevented from observing other birds. Perches were provided and water was available *ad libitum.* Each bird was familiarized with the experimental cages until it fed readily prior to participating in latency tests.

We standardized familiarity with fruit choices prior to latency tests by offering individuals the fruits with which they were to be tested for a 24-hr period, 48 hrs prior to testing. We standardized motivation to feed by providing maintenance diet *ad libitum* to individually held birds for a 24-hr period prior to testing beginning at 1700 hrs 2 days before testing. We removed the maintenance diet at 1700 hrs the day before testing and birds were held without food overnight to encourage feeding during the latency tests. The next morning, at 0800 hrs, we offered birds five fruits for 10-min periods at 20-min intervals. We removed and inspected the fruit to learn whether consumption had occurred at the conclusion of each 10-min period. We calculated the latency period from the time fruit was first offered until consumption occurred. Testing concluded with each bird when it ate or at 1700 hrs if it did not. The latency period was calculated as the time elapsed between first offering fruit and the 10-min time block in which consumption occurred. If a bird did not eat by 1700s hr it was assigned a latency period of 550 min; each bird was tested only once with each invasive fruit.

Responses to Novel Foods.—We limited the difference between novel and familiar foods to a single variable by preparing the novel foods from maintenance diet that was altered by the addition of food coloring. Both foods were presented in containers identical to those used for feeding on a daily basis. We controlled for the possible association of particular colors with foods that the birds already recognized as edible or desirable by selecting colors that our birds were unlikely to have experienced in foods found in the wild (bright teal blue-green: approximate Munsell color 2.5B 8/1 15.180.183; and silvery-purple gray: approximate Munsell color 7.5PB 7/1 177.161.166). We prepared food in a single batch measuring 250-g portions into containers, covering them with plastic wrap pressed onto the surface to prevent discoloration, and freezing them until needed for experimental use. Corresponding batches of familiar food, deep brown in color, were prepared at the same time and also frozen. All food was thawed at room temperature prior to use.

We first examined whether starlings and robins differed in their choices when allowed to select between familiar and novel foods. We used the methods already described (native vs. invasive choice tests, above), except that birds were not exposed to the novel foods prior to testing. Each bird was tested with two novel foods (blue and gray), each of which was presented one at a time in combination with the uncolored maintenance diet. The order of encounter as well as position of the novel food was randomized by coin-toss. No bird was tested more than once with each color. The food first eaten was scored as preferred and a trial ended when a food had been selected. All choice tests began between 0700 and 1100 hrs. Starlings were tested from July to September 2001 while robins were tested in July 2002.

We also tested starling and robin willingness to eat a novel food when no other food was available using latency tests as described previously. We used the same birds as in the choice trials with novel foods; however, birds were tested with only the blue-green novel food. The blue-green food was selected by only one bird in the choice tests, and it was still untested and unfamiliar to all other birds. Latency tests were conducted during August 2002 for both starlings and robins.

Statistical Analysis.—We examined choice test data using binomial probability distributions. Latency data were checked for normality and heterogeneity of variances prior to analysis. These data did not meet the assumptions required for parametric tests and were analyzed using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test, a nonparametric, rank-based equivalent of a two-way ANOVA with replication. Means are reported ±SD and results were considered significant at $P < 0.05$.

RESULTS

Choice Tests with Native and Invasive Fruits.—Birds demonstrated significant preferences for one kind of fruit in five of six experiments presenting pairs of native versus invasive fruits (Fig. 1). European Starlings demonstrated a significant preference for one member of each fruit pair. Invasive fruits were preferred (autumn olive vs. winterberry: $z = 3.16$, $P = 0.002$, $n = 10$; multiflora rose vs. swamp rose: $z = 3.32$, $P = 0.001$, $n = 11$) and were the only fruits eaten in two of three pairings. Only when choosing between glossy buckthorn and highbush blueberry did starlings prefer the fruit of the native plant ($z = -3.16$, $P = 0.002$, $n = 10$) and eat some of both choices in the pair. American Robins significantly preferred the fruits of autumn olive ($z = 2.64$, $P = 0.008$, $n = 7$) and multiflora rose ($z = 2.64$, $P = 0.008$, $n = 7$) to those of native plants to which they were paired. Like starlings, they consumed no winterberry and only one swamp rose fruit. Unlike starlings, when selecting between glossy buckthorn and highbush blueberry, robins displayed no preference ($z = -1.13$, $P = 0.26$, $n = 7$), typically consuming both native and invasive fruits in each trial.

Latency Tests with Invasive Fruits.—European Starlings and American Robins did not differ in their willingness to eat fruits of invasive plants when no other food was available (Scheirer-Ray-Hare extension of Kruskal-Wallis test, $H = 2.23$, df = 1, $P = 0.14$). However, both starlings and robins were significantly more willing to eat fruits of some invasive plants than others ($H = 19.97$, df =

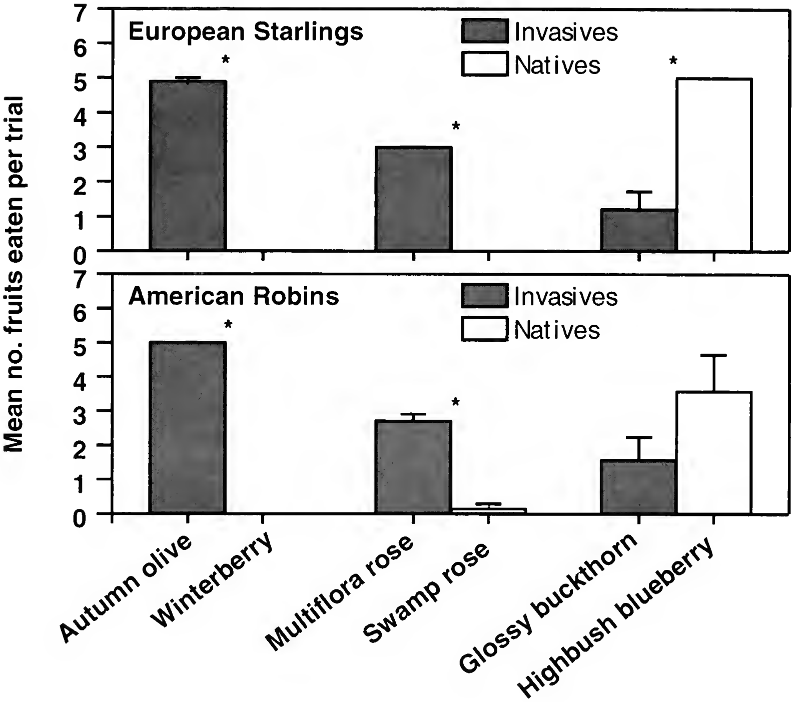

FIG. 1. Mean number of fruits eaten per trial in choice tests by European Starlings and American Robins. Asterisks indicate cases in which birds demonstrated a significant preference for one member of the fruit pair.

2, $P = 0.001$). Starlings began eating autumn olive significantly more quickly than either multiflora rose or Asiatic bittersweet (Bonferroni correction applied to *post hoc* paired Mann-Whitney U-tests, $P = 0.001$ and $P = 0.003$, respectively), and robins began eating autumn olive significantly more quickly than Asiatic bittersweet (Bonferroni correction applied to *post hoc* paired Mann-Whitney U-tests, $P = 0.003$). The interaction between bird and plant species was not statistically significant ($H = 5.93$, df = 2, $P = 0.051$).

Both starlings and robins ate autumn olive fruits willingly, as demonstrated by the mean times it took them to begin eating (Fig. 2; starlings: mean = 23.33 ± 40.00 min, median = 10 min, $n = 9$; robins: mean = 10.00 ± 0 min, median = 10 min, $n = 7$). Starlings were less willing than robins to consume multiflora rose fruits (starlings: mean = 459.00 ± 172.85 min, median = 550 min, $n = 10$; robins: mean = 91.43 ± 202.52 min, median = 10 min, $n = 7$). Six starlings did not eat any multiflora rose fruits during the latency tests; thus, our data provide a minimum estimate of the average time required for starlings to begin eating these fruits. Starlings were more willing to eat Asiatic bittersweet fruits (mean = 253.00 ± 211.40 min, median = 265 min, $n = 10$) than were robins (mean = 417.14 ± 201.88 min, median = 550, $n = 7$). Latency times for robins are a minimum estimate as four robins did not eat any Asiatic bittersweet fruits. While birds were held overnight without food prior to both the choice and latency tests, we suggest the lack of willingness by starlings to feed on multiflora rose fruits in the latency tests was the result of differences in hunger levels as the result of differences in experimental procedures. The day prior to choice tests, groups of starlings were held on the fruits they would be required to choose between, while in the 24 hrs prior to latency tests, starlings were held individually and offered maintenance diet *ad libitum.*

Responses to Novel Foods.—All starlings offered novel and familiar foods simultaneously chose to eat the familiar food, regardless of whether it was paired with the blue-green or gray novel food (binomial test with

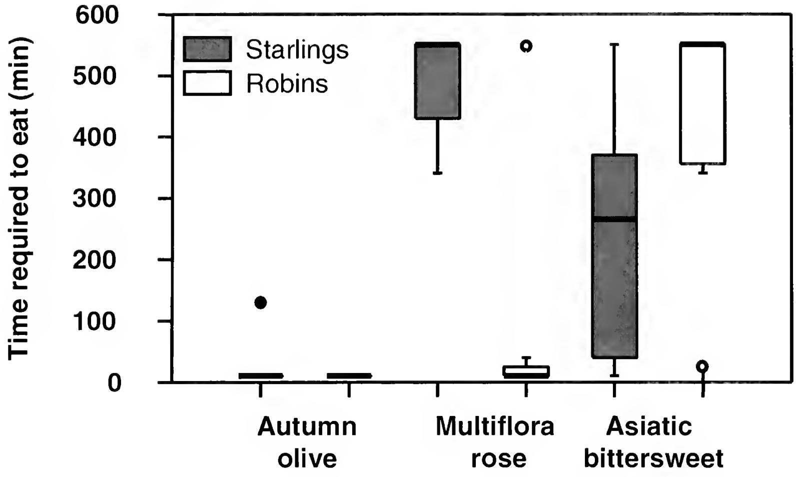

FIG. 2. Time required for European Starlings and American Robins to begin to eat fruits of selected invasive plants. Medians are shown as heavy horizontal lines, first and third quartiles as lower and upper horizontal box edges. Whiskers denote most extreme values within inner fences (1.5 times the distance between the upper and lower quartiles), and outliers are filled circles (starlings), and open circles (robins).

pooled data, $z = 4.69$, $P = 0.001$, $n = 22$). Robins selected the novel food over the familiar food in four of 16 trials, although preference for the familiar food was still significant for this species (binomial test with pooled data, $z = -2.00$, $P = 0.046$, $n = 16$). In three of these four cases, the gray novel food was selected when paired with the familiar food (binomial test, $z = -0.71$, $P = 0.48$, $n = 8$) and, in the last case, the blue-green novel food was selected (binomial test, $z = -2.12$, $P = 0.034$, $n = 8$). Only one robin selected both the blue-green and gray novel foods when paired with the familiar food.

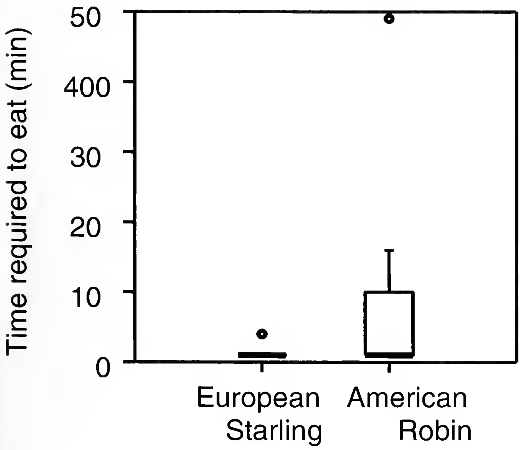

FIG. 3. Time required for European Starlings and American Robins to eat novel food when no other food was available. Medians are shown as heavy horizontal lines, first and third quartiles as lower and upper horizontal box edges. Whiskers denote most extreme values within inner fences (1.5 times the distance between the upper and lower quartiles), and outliers are open circles.

Starlings sampled the novel food in latency tests in an average of 16.7 ± 13.2 min (median = 10, $n = 9$), while robins took 104.3 ± 178.7 min (median = 10, $n = 7$) to do so (Fig. 3). This result was not statistically significant (Mann-Whitney *U*-test, $U = 23.00$, $P = 0.27$), perhaps due to the large variability among robins and the small sample size. The short latency period and low variability in starlings, however, suggests they will typically adopt a novel food more quickly than robins when no other choices are present.

DISCUSSION

Our results provide clear evidence that European Starlings and American Robins exhibit strong and consistent preferences for particular types of fruits. In two of three cases we examined, both avian frugivores preferred fruits of invasive plants to those of native plants. The results of other studies that examined whether avian frugivores prefer fruits of invasive to native plants have produced conflicting results. Sallabanks (1993) found that free-living avian frugivores in Oregon removed the fruits of an invasive hawthorn (*Crataegus monogyna*) at greater rates than fruits of its native congener (*C. douglasii suksdorfii*). Jung (1992) found that captive American Robins preferred fruits of native white mulberry (*Morus alba*) and red-osier dogwood (*Cornus stolonifera*) to those of the invasive Bella honeysuckle (*Lonicera* × *bella*). Whelan and Willson (1994) found that when accessibility was controlled, free-living birds in Illinois preferred fruits of native pokeweed (*Phytolacca americana*) to those of autumn olive. Greenberg et al. (2001) compared fruit removal rates of native American holly (*Ilex opaca*) and invasive Asiatic bittersweet and found no significant difference. These studies suggest that factors affecting choices birds make between invasive and native fruits are complex, vary with the suite of available choices, and depend on the characteristics of both frugivores and fruits involved.

Starlings and robins often made similar choices when choosing between the fruits of a native and an invasive plant, but in latency tests they demonstrated species-specific differences in the time required before beginning to eat invasive fruits. Our experimental design controlled for some fruit characteristics that have been shown to affect fruit choice, such as accessibility (e.g., Denslow and Moermond 1982), abundance (e.g., Sallabanks 1992), and color (Turcek 1963). Other factors, such as nutrient and energy content (e.g., Sorensen 1984), seed characteristics (e.g., Howe and Vande Kerckhove 1980), seed passage rates (e.g., Sorensen 1984), and fruit size (e.g., Wheelwright 1985) have also been shown to influence fruit selection. In addition, the digestive physiology of frugivores is important to understanding feeding choices. For instance, the ability to digest lipids (Witmer and Van Soest 1998, Lepczyk et al. 2000), sugar composition of fruits (e.g., Martínez del Rio et al. 1988), and the presence of secondary plant compounds (e.g., Guglielmo et al. 1996), may affect a bird's abilities to use ingested food and influence feeding choices. Some of the fruits in this study persisted on the plants throughout the winter, and all were carbohydrate rather than lipid-rich (Table 1).

The chemistry of the sugars in the fruits considered in this study is unknown: most sugars in bird-dispersed fruits are fructose and glucose (Baker et al. 1998). Neither starlings (Martínez del Rio et al. 1988) nor robins (Karasov and Levey 1990) are able to digest sucrose. We have little reason to suggest that sugar composition differentially affected starling and robin choices although the percentage of energy provided by sugars may have influenced frugivore choices. Data compiled from the literature on the characteristics of the fruits in our study (Table 1) suggests that neither starlings nor robins favored or avoided the fruits used in choice tests on the basis of characteristics such as fruit mass, seed mass, pulp: seed ratio, caloric content, or percent lipids. However, our data revealed several patterns. In choice tests, starlings selected fruits with the highest percentage of soluble carbohydrates, while robins tended to select fruits with the highest percentage of protein. Starlings exhibited the shortest latencies for fruits with the highest pulp:seed ratios and robins began eating those with the lowest seed masses most quickly. We predicted that, when allowed to choose between a familiar and a novel food, both species would select the familiar food. All starlings chose the familiar food; however, three of eight robins selected the novel food in at least one trial. Previous studies by Jung (1992) and Willson (1994) also found variation in food choice among individual robins when tested with real and artificial fruits. We predicted that starlings in latency tests would test the novel food significantly more quickly than robins. Starlings required a mean time of only 16.7 ± 13.2 min to test the novel food and all birds ate within 40 min. The short latency period and consistency of response suggests that when no familiar food sources are available, starlings will readily switch to new food sources. Robins waited on average six times as long as starlings before testing the novel food and displayed much greater individual variation in the time required (104.3 ± 178.7 min). Small sample sizes, large standard deviation for our robin group, and the need to use nonparametric tests resulted in low test power (0.164) and may have contributed to our inability to detect a significant effect.

These results suggest the different strategies starlings and robins use when encountering novel foods may result in different roles in the dispersal of the seeds of newly introduced plants. Starlings consistently chose the familiar food when available but, when not available, they were consistently willing to try the alternative. Robin responses were less consistent and more variable among individuals, but at least some robins were willing to test novel foods regardless of the presence of familiar food. Taken together, our results indicate the availability of both initial seed-dispersal services for newly introduced plants and consistent dispersal services once a plant population is established.

Attraction of frugivores is the first step in seed dispersal for fleshy-fruited plants and preferences for invasive fruits are unlikely to benefit populations of native flora. The factors which drive the preferences for invasive fruits we observed were outside the scope of this study, but are important targets for further study. Further examination of patterns of fruit selection by avian frugivores is needed if we wish to understand precisely which fruit characteristics promote invasiveness in introduced fleshy-fruited plants.

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AVIAN BIOGEOGRAPHY OF AMAZONIAN FLOODED FORESTS IN THE RIO BRANCO BASIN, BRAZIL

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ABSTRACT.—Flooded forests represent an important part of Amazonian diversity, yet the distribution, ecology, and evolutionary history of the avifauna of these forests have received little attention. We conducted ornithological surveys in the Rio Branco Basin, which is entirely in the Brazilian State of Roraima. In this paper, we discuss the presence of 20 bird species recorded along the lower Rio Branco, 16 of which represent new records for the State of Roraima and the entire Rio Branco Basin. Among our most interesting records are four species of white-water river specialists (*Synallaxis propinqua*, *Stigmatura napensis*, *Serpophaga hypoleuca*, and *Conirostrum bicolor*) that have populations on the lower Rio Branco, isolated from other Amazonian white-water river systems by the black waters of the Rio Negro where they do not occur. We also discovered new localities for the endemic and endangered Rio Branco Antbird (*Cercomacra carbonaria*), doubling the size of its known range. We discuss the implications of these records in a biogeographic perspective for better understanding the distributional patterns of the flooded-forest avifauna in Amazonia. *Received 11 May 2006. Accepted 12 December 2006.*

The Amazon Basin contains the most spectacular river system on earth. Not only is the Amazon River the longest and largest river in the world, but some of its tributaries also rate among the 10 largest (Goulding et al. 2003). These rivers create the Amazonian flood plains, a mosaic of habitats which remain flooded for as much as 8 months every year (Junk 1989). These seasonally flooded habitats, known in Brazil as *várzeas* and *igapós*, include floating meadows, sandbar scrub, river-edge forest, and tall flooded forest each hosting a diverse and highly specialized avifauna that accounts for at least 15% of Amazonia's overall non-aquatic bird diversity (Remsen and Parker 1983).

Despite the continental extent of this ecosystem, which ranges thousands of kilometers across northern South America, from the base of the Andes to the Atlantic Ocean, the distribution, ecology, and evolutionary history of its avifauna have been poorly studied. Until recently, flooded forests have not captured the attention of avian biogeographers (Cohn-Haft et al. in press), who have focused mostly on describing bird distribution patterns and generating evolutionary hypotheses for Amazonian *terra firme* forests (e.g., Sick 1967, Haffer 1969, Nores 1999). We attribute this lack of interest in the biogeography of flooded forest birds, in part, to the general assumption that these birds, by living in dynamic and relatively ephemeral habitats, must have strong dispersal abilities. Strong dispersal abilities in continuous, linear environments should not favor genetic isolation and differentiation of populations, leading to the expectation of widespread species with little or no geographic variation (Remsen and Parker 1983). The lack of precise distributional data for *várzea* birds has also prevented ornithologists from making historical interpretations that go beyond a handful of species (e.g., Haffer and Fitzpatrick 1985, Haffer 1997, Isler et al. 1999, Aleixo 2006).

The Rio Branco is unique in Amazonia, because it is a nutrient-rich, semi-muddy river, surrounded by black-water rivers (poor in sediments and nutrients, but rich in organic matter). The 'color' of the water has important ecological implications, because muddy and semi-muddy rivers (hereafter 'white-water' rivers) differ from black-water rivers not only in the amount of sediments they carry, but also in the structure and composition of the

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vegetation along their margins (Klinge and Furch 1991), affecting the species richness and composition of its associated avifauna (Rosenberg 1990, Petermann 1997, Borges and Carvalhaes 2000). Many widespread flooded-forest birds occur in riverine habitats created by both types of rivers, but some are restricted to either black-water or white-water rivers. White-water river specialists that are present on the Rio Branco are necessarily isolated from other white-water drainages of Amazonia, potentially allowing genetic and population differentiation.

The Rio Branco Basin lies in a region of high habitat heterogeneity and of great ecological and biogeographical interest, important for our understanding of distributional patterns of Amazonian birds (Naka et al. 2006). The only major ornithological explorations on the Rio Branco until the mid 20th century were those of Natterer in 1831 and 1832 (von Pelzeln 1868–1871). More recently, Stotz (1997) and Zimmer et al. (1997) surveyed the river, but like Natterer only explored the upper Rio Branco, where river-created habitats consist of narrow stretches of gallery forest. The avifaunas of gallery and flooded forests are generally distinct; the former being more closely related to dry forests in the savannas than to Amazonian flooded forests. The first comments on the birds of the lower Rio Branco were published by Pacheco (1995) after a short visit to the mouth of the river and by Santos (2004), who worked on several river islands near Caracaraí.

This paper reports our most interesting observations obtained during several avifaunal surveys on the lower Rio Branco since 1990, including several significant range extensions and 16 species new to the Rio Branco Basin and the State of Roraima. We discuss the biogeographical implications of these records and call attention to the presence of previously overlooked and possibly isolated populations of white-water river specialists on the Rio Branco.

METHODS

Study Area.—The Rio Branco Basin is within the Brazilian State of Roraima (Fig. 1) and the river is the largest tributary of the Rio Negro, itself the second-largest tributary of the Amazon and the largest black-water river in the world. The basins of the Rio Negro and Rio Branco jointly contribute nearly 15% of the total annual discharge of the Amazon River and occupy an area of roughly 700,000 km^2, more than 10% of the Amazon Basin (Goulding et al. 2003). The Rio Branco is not as turbid as the Amazon or the Madeira rivers, but its waters contrast strongly with the dark waters of the Negro. On satellite imagery, this "meeting of the waters" can be seen for more than 50 km downstream from their confluence.

We divide the Rio Branco in two main geographical and ecological regions: the upper and lower Rio Branco with the city of Caracaraí (01° 50′ N) as the dividing point. About 70 km north of Caracaraí, coinciding with the confluence of the Rio Branco and the Rio Mucajaí, rainfall decreases sharply (Barbosa 1997) and soil conditions change drastically (Brown and Prance 1987). Savannas replace lowland Amazonian forests in this region and, along the rivers, gallery forests replace flooded forests. We have not sampled the Rio Branco between Caracaraí and Mucajaí, and do not know how gradually these changes occur. However, apparently many flooded-forest bird species readily found around Caracaraí are not present in the gallery forests of the Rio Mucajaí or Rio Branco from Mucajaí north.

The terms *várzea* and *igapó* are local terms used to describe flooded forests and are often used interchangeably by local inhabitants. Here, we follow Prance (1979) using these terms to distinguish forests based on the kind of water that floods them: *várzea* for forests flooded by white (muddy) waters and *igapó* for forests flooded by black (translucent, acidic) waters. The banks of the lower Rio Branco are covered by extensive *várzeas*, whereas many of its tributaries (i.e., Água Boa do Univini, Iruá, and Ajarani) are black-water rivers, whose margins are covered by *igapó*.

The Rio Branco has an average river-level fluctuation of 5.7 m, which is enough to flood large areas along the river, and to 'dam' smaller tributaries (Goulding et al. 2003). Vegetation structure and floristic composition depend on the duration and level of the flooding; areas flooded for longer periods tend to support fewer tree species (Junk 1989). The *várzeas* of the Rio Branco have a well-developed canopy reaching 20–25 m in height, and the un-

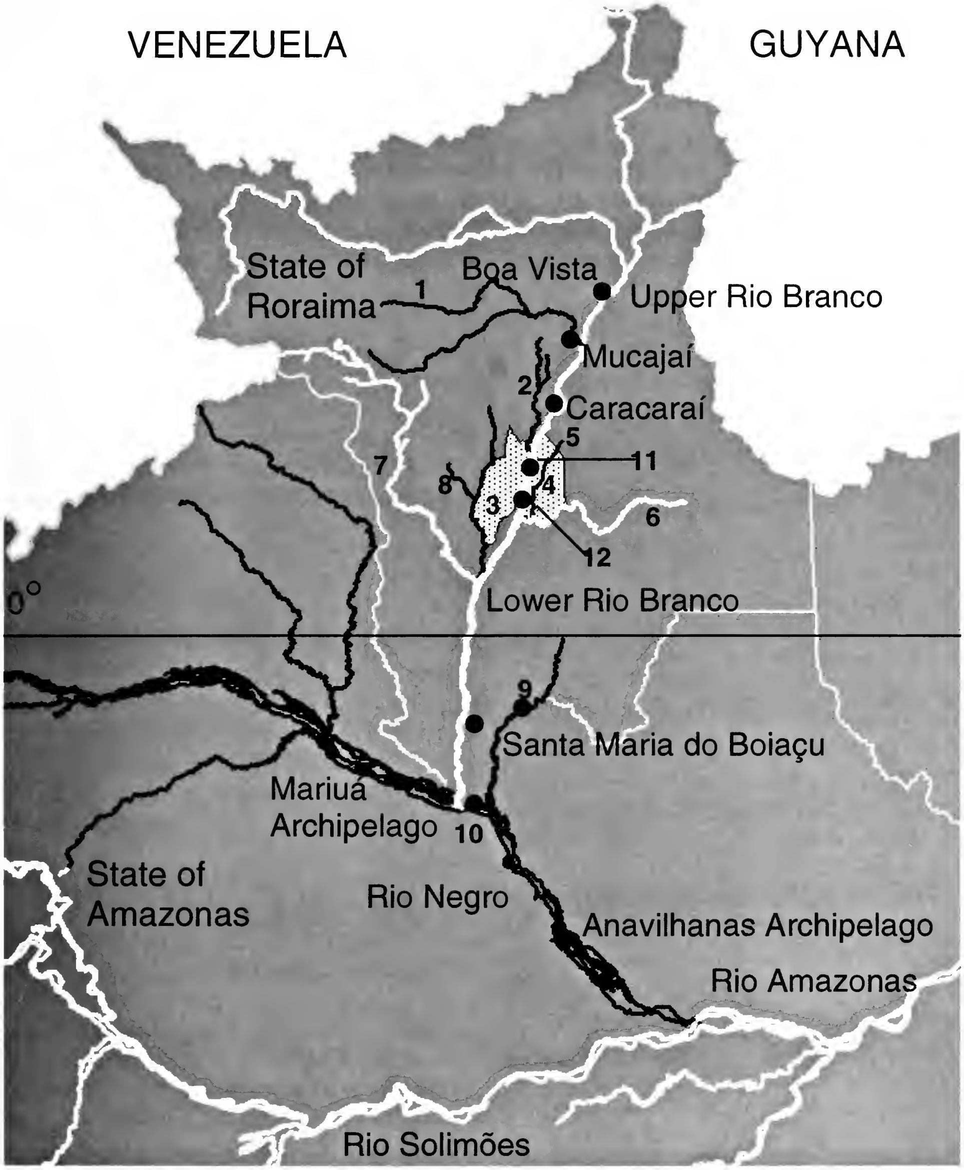

FIG. 1. The Rio Branco Basin and study localities, enclosed by the Brazilian State of Roraima, and included within the Rio Negro Basin. White-water rivers are white; black-water rivers are black. Stippled areas represent reserves. Numbers represent the following rivers or localities: (1) Rio Mucajaí, (2) Rio Ajaraní, (3) Niquiá Ecological Station, (4) Viruá National Park, (5) Rio Iruá, (6) Rio Anauá, (7) Rio Catrimani, (8) Rio Água Boa do Univini, (9) village of Samaúma on the Rio Jauaperí, (10) Paraná da Floresta, (11) Marari Island, and (12) Inajatuba island. Digital data obtained from Ministério do Meio Ambiente (2001).

derstory is generally open and poorly developed. Tree species diversity and complexity of vertical structure on river islands increase as an island ages (Robinson and Terborgh 1997) creating a series of successional stages that range from sandbars to river-edge forest (dominated by *Cecropia*) to mature *várzea* forest, which has the highest number of tree species (Remsen and Parker 1983). *Igapós* are usually associated with sandy soils and have fewer tree species than *várzea* forests, narrower tree diameters, and a lower canopy height (15–20 m). The physiognomy and floristic composition of the *igapó* resemble that of white-sand forests (Anderson 1981).

Field Work.—AW visited the lower Rio Branco near the mouth of the river on 10–11 June and 22–24 December 1990, 6–7 April 1991, 19–20 August 1993, 25–26 January and 25–26 July 1994, 24–25 March and 15–16 July 1995, and 9–10 June 1996. MCH made a short visit to the mouth of the Rio Branco on 6 July 1999. In 2001 and 2006 we joined three expeditions sponsored by the *Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis* (IBAMA) to survey the avifauna of the lower Rio Branco and some of its tributaries. Between 6 and 11 July 2001, LNN and MFT covered ~100 km of the Rio Branco (from Santa Maria do Boiaçu to the mouth of the river), a short stretch of the Rio Negro influenced by the Rio Branco (Paraná da Floresta), and the west bank of the Rio Jauaperí (from its mouth to the village of Samaúma). Between 5 and 18 October 2001, LNN and JMB covered ~170 km of the Rio Branco from Caracaraí south to the mouth of the Rio Catrimani and some Rio Branco tributaries (Água Boa do Univini, Iruá, Anauá, and Ajarani rivers). Between 1 and 15 October 2006, LNN and MCH, accompanied by Marcelo dos Santos Jr. and Catherine L. Bechtoldt, studied ~80 km of the Rio Branco from Caracaraí to the confluence with the Rio Anauá, and another 35 km up the white-waters of the Rio Anauá and a similar distance along the black-waters of the Rio Iruá.

We usually conducted bird surveys during early morning (0500–1200 hrs), late afternoon (1500–1830 hrs), and sporadically at night using binoculars and tape-recorders. We explored river-created habitats (*várzea* and *igapó*) using small motorboats, which allowed access to the forest interior. LNN and MCH collected bird specimens, housed at the *Instituto Nacional de Pesquisas da Amazônia* (INPA) Bird Collection in Manaus, Brazil. Tape-recordings by LNN and MCH are archived at the INPA Bird Collection; those by AW are at the British Library National Sound Archive. Taxonomy and species nomenclature follow the Brazilian Ornithological Records Committee (Comitê Brasileiro de Registros Ornitológicos 2006).

RESULTS

We present details of 20 species recorded during our fieldwork which represent either new records for the Rio Branco Basin and the State of Roraima (species marked with an asterisk), or note-worthy range extensions.

Species Accounts

**Leucopternis schistaceus* (Slate-colored Hawk).—AW found two single individuals on river islands on the lower Rio Branco (15 and 27 km north of the river's mouth) on 10 June 1990 and 7 April 1991, respectively. In October 2001 LNN and JMB observed and tape-recorded two birds in tall *várzea* forest along the east bank of the lower Rio Branco (01° 36′ 20″ N, 61° 13′ 08″ W) at Viruá National Park. This species seems to be restricted to tall flooded forests in Brazil (Bierregaard 1994) and probably occurs in the State of Roraima only along the lower Rio Branco.

**Asio stygius* (Stygian Owl).—AW observed one bird perched on a sand bar of a river island 25 km north of the mouth of the Rio Branco on the night of 22 December 1990. In subsequent visits to that island the following day and following year (April 1991) AW repeatedly found an individual there (presumably the same bird). This species is widely distributed from Mexico to Argentina, but seems to be rare and local (Marks et al. 1999). This owl generally inhabits savannas in Amazonian Brazil, but in recent years AW has obtained several records from areas associated with black-water rivers and river islands.

**Monasa nigrifrons* (Black-fronted Nunbird).—AW found this species along the lower Rio Branco on 23 December 1990 and in successive trips to the same general area. Subsequently, LNN, JMB, and MFT observed and tape-recorded several individuals in *várzea* forest along both banks of the lower Rio Branco. Our records ranged from the mouth of the river north to the island of Inajatuba (01° 17′ 22″ N, 61° 18′ 04″ W), nearly 60 km south of Caracaraí. This species is widespread in Amazonia, mostly restricted to flooded forests (Rasmussen and Collar 2002), but seems to be restricted in the State of Roraima to the *várzeas* of the lower Rio Branco, with no known records from gallery forests further north or from Venezuela (Hilty 2003).

**Myrmotherula klagesi* (Klages' Antwren).—AW heard and observed several pairs in mature *várzea* forest ~20 km north of the mouth of the Rio Branco on 23 December 1990. Birds were subsequently tape-recorded by AW along both banks of the Rio Jauaperí in August 1993 and other sites along the lower Rio Branco in June 1993 and July 1995. MCH tape-recorded the species near the mouth of the Rio Branco in July 1999, and in July and October 2001, LNN and MFT, and LNN and JMB, respectively, documented its presence throughout the lower Rio Branco, obtaining tape-recordings from the mouth of the river as far north as the island of Inajatuba, 300 km to the north. On 6 October 2006 MCH tape-recorded and collected a male from a river island on the Rio Branco, opposite the mouth of the Rio Anauá, representing the first specimen for the State of Roraima. Previously, this species was known to occur on the lower Rio Negro and along the Amazon, including the Rio Madeira and the mouth of the Rio Tapajós (Zimmer and Isler 2003). Our records extend the known distribution of *M. klagesi* well into the Rio Branco Basin and more than 300 km northward from previous known sites on the Rio Negro.

**Myrmotherula assimilis* (Leaden Antwren).—AW observed this species in tall *várzea* forest ~20 km north of the mouth of the Rio Branco on 10 June 1990 and several other times in the same general area. In July and October 2001, LNN and MFT, and LNN and JMB, respectively, tape-recorded this species throughout the lower Rio Branco, as far north as the island of Inajatuba, and also along the Anauá and Jauaperí rivers. This species is known to be widespread in flooded forests throughout much of Amazonia (Zimmer and Isler 2003), but was previously unrecorded from the Rio Branco Basin.

**Cercomacra nigrescens* (Blackish Antbird).—MCH tape-recorded this species in Roraima at the mouth of the Rio Branco on 6 July 1999. Subsequently, in July and October 2001, LNN and MFT, and LNN and JMB, respectively, saw and tape-recorded several individuals in mid-successional vegetation on riverine islands and forest edges along both banks of the lower Rio Branco from the mouth of the river north to the island of Inajatuba where it was fairly common. Additionally, LNN and MFT tape-recorded several individuals along the Paraná da Floresta on the Rio Negro. On 15 October 2006 LNN tape-recorded and collected a pair on the left bank of the Rio Branco (01° 31′ 06″ N, 61° 14′ 25″ W). Three other individuals had been collected earlier by M. P. D. Santos from Viruá National Park and São João da Baliza in August 2002 and January 2003, respectively. Most of the known range of *C. nigrescens* is restricted to areas south of the Amazon from eastern Colombia to the Brazilian State of Pará (Zimmer and Isler 2003). The only known populations north of the Amazon are represented by the nominate race, which occurs in Surinam, French Guiana, and along the north bank of the Amazon in the Brazilian State of Para (Pinto 1978, Haverschmidt and Mees 1994). These are the first published records of *C. nigrescens* from the Rio Branco and are separated by ~360 km and more than 600 km from nearest localities to the south and north, respectively, apparently representing a disjunct population.

Cercomacra carbonaria (Rio Branco Antbird).—This taxon was considered to be strictly associated with gallery forests along the upper Rio Branco and some of its tributaries (Stotz 1997, Zimmer et al. 1997, Santos 2003, Zimmer and Isler 2003). In July and October 2001, LNN and MFT, and LNN and JMB, respectively, found and tape-recorded several individuals along the lower Rio Branco where it was locally common in young riverine islands dominated by *Cecropia* spp. In October 2006, LNN and MCH also found the species to be common on riverine islands from Caracaraí south to the mouth of the Rio Anauá. Our records extend the known range of this species south of Caracaraí (previously considered its southernmost limit) to only 13 km north from the mouth of the Rio Branco (01° 16′ 19″ S, 61° 50′ 21″ W). We do not expect to find this species anywhere outside the Rio Branco Basin or in adjacent black-water rivers where successional river islands do not occur. We failed to find *C. carbonaria* in tall *várzea* forests where *C. nigrescens* was present suggesting that species interactions and habitat preferences may limit its distribution within the Rio Branco Basin. Our records along the lower Rio Branco suggest that *C. carbonaria* has greater ecological plasticity than previously thought and represent a range extension of more than 300 km southward, doubling the size of its global distribution. At present, *C. carbonaria* is considered Vulnerable to extinction by BirdLife International (2000), but was recently excluded from the Brazilian list of threatened birds (Ministério do Meio Ambiente 2003) based on lack of data. More recently, Vale et al. (in press) suggested downlisting the species to near-threatened, in part due to the significant range extensions here presented.

**Sclateria naevia* (Silvered Antbird).—AW found a vocalizing male 25 km north of the mouth of the Rio Branco on 16 July 1995. Subsequently, LNN and MFT observed and tape-recorded a pair along a dry stream near São João da Baliza at the edge of the Wai-Wai Indian Reservation (01° 05′ 21″ N, 59° 56′ 37″ W) in March 2001 and, in October 2006, LNN and MCH found several birds along the Rio Anauá. These are the first records for the region and fill what had appeared as a somewhat inexplicable gap in its distribution (Zimmer and Isler 2003).

Synallaxis propinqua (White-bellied Spinetail).—AW found several individuals vocalizing in early-successional vegetation on a river island 27 km north of the mouth of the Rio Branco on 21 March 1993. One individual was tape-recorded by Pacheco (1995) in October 1993 near the mouth of the Rio Branco. In October 2006, LNN and MCH found several individuals on a young river island along the Rio Branco, opposite the mouth of the Rio Anauá, and on two other river islands. On 14 October 2006 MCH tape-recorded and collected one male on the island of Marari (01° 28′ 42″ N, 61° 14′ 58″ W) where two pairs were building nests. Previous to these records, this spinetail was known to occur locally in early-successional growth on river islands along the Amazon River and some of its white-water tributaries (Remsen 2003). Our records not only document the presence of this species in the Rio Branco Basin, but also suggest the presence of a breeding population isolated from the main populations distributed contiguously along the Amazon River and its tributaries.

**Cranioleuca gutturata* (Speckled Spinetail).—LNN and JMB found and tape-recorded one individual in mature *várzea* forest at the Niquiá Ecological Station (00° 50′ 08″ N, 61° 25′ 45″ W) on 6 October 2001. On 9 October 2006 LNN tape-recorded and collected a male in tall *várzea* forest along the Rio Anauá (00° 57′ 20″ N, 61° 09′ 22″ W). These are the first records from the Rio Branco Basin although this species is relatively widespread in Amazonian flooded forests and is present along the lower Rio Negro (Cintra et al. 2007).

**Hemitriccus minor* (Snethlage's Tody-tyrant).—AW saw and tape-recorded one individual 20 km north of the mouth of the Rio Branco on 20 August 1993. Subsequently, MCH found this species in Roraima at the mouth of the Rio Branco in July 1999, and in July and October 2001, LNN and MFT, and LNN and JMB, respectively, found it along most of the lower Rio Branco and other blackwater tributaries, including the Água Boa do Univini and Ajaraní rivers (our northernmost locality in Roraima). Our records seem to refer to the race *pallens*, which is a flooded-forest inhabitant common along the middle and lower Rio Negro.

Serpophaga hypoleuca (Riverside Tyrannulet).—AW found a pair on a young river island 27 km north from the mouth of the Rio Branco on 21 March 1993. This species was also recorded on the lower Rio Branco by Pacheco (1995). Prior to these records, this early-successional vegetation inhabitant was known from several white-water rivers in the Amazon Basin, but not from the Rio Branco or the Rio Negro basins (Fitzpatrick 2004).

**Stigmatura napensis* (Lesser Wagtail-tyrant).—AW found a pair in early-successional vegetation on a river island 27 km upstream from the mouth of the Rio Branco on 21 March 1993. On 13 October 2006 MCH and LNN tape-recorded and collected a pair in early successional vegetation on the island of Marari. Several other pairs were located on the same island the following day. The female collected had unshelled eggs in the ovary, suggesting that individuals were reproducing on this island. Prior to our records, the Amazonian form (nominate race) of this species was known to occur exclusively along white-water Amazonian rivers south of the Amazon, especially on newly-formed sandbars with bushes of the genus *Tessaria* (Fitzpatrick 2004). We believe this species is absent from the Rio Negro and that birds recorded on the Rio Branco represent an isolated population. Another isolated population was recently found on the upper Orinoco River (Hilty 2003).

**Inezia subflava* (Amazonian Tyrannulet).—AW heard several pairs in flooded vegetation at a lake edge 20 km north of the mouth of the Rio Branco on 23 December 1990 and 23 March 1995. MCH, LNN, and MFT encountered and tape-recorded this species in Viruá National Park in March 2001. Subsequently, in July and October 2001, LNN and MFT, and LNN and JMB, respectively, found *I. subflava* to be fairly common in *várzea* and *igapó* edges along the lower Rio Branco and some black-water tributaries such as the Água Boa do Univini, Iruá, and Jauaperí rivers. Previous specimens from the State of Roraima collected by Natterer (von Pelzeln 1868–1871), Pinto (1966), Emílio Dente (held at Museu Paraense Emílio Goeldi, MPEG), and D. F. Stotz (held at the Field Museum of Natural History) were taken from the upper Rio Branco (and other rivers within the savannas domain) and apparently refer to *I. caudata*, now considered a separate species (Zimmer and Whittaker 2000). Our records represent the first for *I. subflava* on the Rio Branco and in the State of Roraima. *Inezia subflava* (a flooded-forest inhabitant) and *I. caudata* (a gallery forest species) seem to replace each other ecologically and geographically, with the region of turnover somewhere near Caracaraí.

**Conopias trivirgatus* (Three-striped Flycatcher).—AW saw a pair at the mouth of the Rio Jauaperí on 25 July 1994. Subsequently, AW tape-recorded a few individuals in July 1995 in transitional *várzea* forest ~20 km north of the mouth of the Rio Branco. The distribution of this species is poorly known with several disjunct populations throughout tropical South America (Fitzpatrick 2004).

**Schiffornis major* (Várzea Schiffornis).—AW heard and observed several birds in *várzea* forest near the mouth of the Rio Branco on 7 April 1991. In October 2001, LNN and JMB saw and tape-recorded individuals in tall *várzea* along the lower Rio Branco (00° 50′ 08″ N, 61° 25′ 45″ W) and in *igapó* along the Rio Água Boa do Univini. One bird was collected in Viruá National Park in August 2002 by M. P. D. Santos (held at MPEG) representing the first specimen for the State of Roraima. Several other birds were also heard along the Rio Anauá by LNN and MCH in October 2006 indicating the presence of this species was previously overlooked in the region.

**Hylophilus semicinereus* (Gray-chested Greenlet).—AW heard one bird vocalizing near the mouth of the Rio Branco on 21 December 1990. Subsequently, in July 2001, LNN and MFT observed and tape-recorded several individuals in tall *várzea* and *igapó* forest along the lower Rio Branco and Rio Jauaperí and, in October 2001, LNN and JMB tape-recorded several individuals within the Niquiá Ecological Station and Viruá National Park. On 9 October 2006 LNN tape-recorded and collected a male from a *campinarana-várzea* transition zone on the right bank of the Rio Anauá (00° 57′ 33″ N, 61° 09′ 30″ W), finding several other individuals along this river and the Rio Iruá. This species is relatively abundant along the Rio Negro and our records fill a sampling gap in its distribution (Ridgely and Tudor 1989).

Conirostrum bicolor (Bicolor Conebill).—LNN and MFT found and tape-recorded two individuals on a river island (01° 16′ S, 61° 50′ W) dominated by *Cecropia*. On 6 October 2006 MCH tape-recorded and collected a male from a group of three birds on an early successional river island on the Rio Branco opposite the mouth of the Rio Anauá. LNN and MCH found this species to be abundant on other river islands between Caracaraí and the mouth of the Rio Anauá suggesting that *C. bicolor* has permanent populations along this stretch of the river. This species has two distinct populations in the Neotropics; one inhabiting mangroves in coastal areas in northern South America and the other inhabiting early-successional vegetation in Amazonia, mainly along the Amazon and some tributaries (Ridgely and Tudor 1989). This species has been previously recorded along the lower Rio Branco by Pacheco (1995) and our records further extend its distribution 260 km to the north, representing the northernmost localities within the Amazon Basin.

**Ammodramus aurifrons* (Yellow-browed

Sparrow).—AW saw two pairs along the edge of a river island 27 km north from the mouth of the Rio Branco on 14 April 1991. Subsequently, in July 2001, LNN and MFT saw and tape-recorded several individuals around the villages of Floresta and Samaúma. In October 2001, LNN and JMB found this species to be locally common along sand-banks and sand-bar scrub on river islands along the lower Rio Branco from the mouth of the river extending to 50 km south of Caracaraí (01° 36′ 19″ N, 61° 13′ 27″ W). On 13 October 2006, LNN tape-recorded and collected a male on a sandy beach on a river island on the Rio Branco (01° 14′ 00″ N, 61° 19′ 01″ W). These records indicate this species is widespread in the region and was previously overlooked due to a sampling gap.

**Sicalis columbiana* (Orange-fronted Yellow-finch).—AW found several individuals along the edge of a river island on the lower Rio Branco on 21 December 1990. Subsequently, in July 2001, LNN and MFT saw and tape-recorded more than 20 individuals at the village of Floresta on the Paraná da Floresta. These seem to represent the first and only records of its occurrence within the Rio Branco Basin and the State of Roraima.

DISCUSSION

Our studies along the lower Rio Branco revealed that south of Caracaraí, the avifauna associated with the river floodplains is represented by typical flooded-forest species, similar to those in the Anavilhanas Archipelago and the lower Rio Negro (Cintra et al. 2007). Environmental variables such as soil, flooding regimes, and rainfall differ between the lower Rio Branco and the upper portions of the river where tall *várzea* forests are replaced by gallery forests. Bird species composition on the lower Rio Branco is generally similar to that of other Amazonian rivers, such as the Amazon, Madeira, and the lower Rio Negro. The avifauna of the upper Rio Branco, however, seems to be more closely related to gallery and dry semi-deciduous forests typical of the savannas of northern Roraima, Guyana, and Venezuela. The transition zone between the two habitats seems to be quite abrupt, occurring within the 70-km stretch between Caracaraí and the mouth of the Rio Mucajaí, coinciding with the region where savannas replace humid forests less than 100 km south of Boa Vista.

Most typical *várzea* bird species such as *Leucopternis schistaceus*, *Monasa nigrifrons*, *Xiphorhynchus kienerii*, *Thamnophilus nigrocinereus*, *Myrmotherula klagesi*, *M. assimilis*, *Myrmoborus lugubris*, and *Hemitriccus minor* seem to reach their northernmost limit in this area. The shift in habitat seems also to be responsible for ecological substitutions between closely related taxa from *várzea* and gallery forests (i.e., *Inezia subflava* and *I. caudata*, and *Ammodramus aurifrons* and *A. humeralis*).

The Rio Branco is unique in representing a white-water river surrounded by black-water drainages including the Negro, Jauaperí, Agua Boa do Univini, Ajarani, and Iruá rivers (Fig. 1). Despite the high similarity between avian communities of the *várzeas* of the Rio Branco and the tall *igapó* of the lower Rio Negro, several elements typical of Amazonian white-water rivers are present on the Rio Branco, but seem to be absent from the entire Rio Negro and its black-water tributaries. We discovered populations of *Cercomacra nigrescens* and *Stigmatura napensis* along the lower Rio Branco, and also confirmed the presence of species previously reported from the mouth of the Rio Branco by Pacheco (1995), such as *Synallaxis propinqua*, *Serpophaga hypoleuca*, and *Conirostrum bicolor*. These species, with the exception of *Cercomacra nigrescens*, which also occurs in *terra firme* forest in part of its range, are typical white-water river-island specialists (Ridgely and Tudor 1989, 1994; Rosenberg 1990; Robinson and Terborgh 1997; Remsen 2003). Repeated records from the area since 1993 suggest these species maintain stable populations locally, rather than representing vagrants or dispersing individuals. Supporting this hypothesis are data that we obtained of unequivocal breeding evidence for *Stigmatura napensis* and *Synallaxis propinqua*.

Most *várzea* birds are believed to be excellent dispersers (Remsen and Parker 1983) and these abilities should be enhanced by having linear and uninterrupted habitats. The existence of isolated populations of white-water specialists along the lower Rio Branco could either be the result of remarkably long-distance dispersal or represent relict populations from once-continuous habitats. Whether these populations are old or relatively recent, their isolation provides an opportunity for genetic differentiation and endemism in *várzea* forest.

Geomorphological data are still equivocal on past connections of Amazonian rivers, but fish communities of the Rio Branco seem to be more closely related to those of the Amazon River than to those of the Rio Negro (Janzen Zuanon, pers. comm.). Recent Parsimony Analysis of Endemicity (PAE) for characiform fishes produced an area of purported endemism including the Rio Branco, the lower Rio Negro, and the lower Amazon excluding the upper Rio Negro and other portions of the Amazon River (Hubert and Renno 2006). This implies the lower Rio Negro may not be as strong a barrier for these fishes as we believe it is for white-water specialist birds. Rossetti et al. (2005) suggested the existence of a body of water connecting the upper Amazon River and the Rio Branco during the late Pleistocene, a scenario that could explain the existence of recently isolated populations of white-water specialists on the Rio Branco. The extent, age, size, and genetic distinctiveness of these avian populations have not been studied, but represent important data for our overall understanding of the evolutionary history of Amazonian rivers and related flooded forests.

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The Wilson Journal of Ornithology 119(3):450–454, 2007

NEW LOCALITIES FOR THE BLACK-FACED HAWK (*LEUCOPTERNIS MELANOPS*) SOUTH OF THE AMAZON RIVER AND DESCRIPTION OF THE IMMATURE PLUMAGE OF THE WHITE-BROWED HAWK (*LEUCOPTERNIS KUHLI*)

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ABSTRACT.—The Black-faced Hawk (*Leucopternis melanops*) and White-browed Hawk (*L. kuhli*) are forest-based, Amazonian raptors whose distributions have been considered to be mutually exclusive north and south of the Amazon River, respectively. The occurrence of *L. melanops* south of the river was first indicated by a specimen collected by A. M. Olalla on the lower Tapajós River >70 years ago. The provenience of this specimen has been contested by diverse authors but both species were recently captured at localities along the lower Tapajós, corroborating the coexistence of *L. melanops* and *L. kuhli* in this region. We present four new specimen localities for *L. melanops* in southern Amazonia, greatly amplifying its known distribution. We also describe the immature plumage of *L. kuhli* based on three specimens that had been identified as *L. melanops*. *Received 20 March 2006. Accepted 11 November 2006.*

The genus *Leucopternis* comprises 10 forest hawk species distributed from southern Mexico to northern Argentina and Uruguay. Six occur in Brazil: White Hawk (*L. albicollis*), Slate-colored Hawk (*L. schistaceus*), White-browed Hawk (*L. kuhli*), and Black-faced Hawk (*L. melanops*) in Amazonia, and the Mantled Hawk (*L. polionotus*) and the endemic White-necked Hawk (*L. lacernulatus*) in the Atlantic forest (Thiollay 1994). Despite the widespread distribution of these species, the ranges of some remain poorly known and the majority of the scarce available data on natural history is anecdotal (Bierregard 1995, Martuscelli 1996). A molecular systematics study including all recognized species of *Leucopternis* indicates the genus is polyphyletic (Amaral et al. 2006) and actually represents at least three independent lineages.

Leucopternis melanops and its sister species *L. kuhli* (Amaral et al. 2006) are the smallest members of the genus (total length ~40 cm) and were considered conspecific by Pinto (1978). Their adult plumages are similar with white belly, dark back, and dark tail with a single subterminal white band. The adult plumage of *L. melanops* can be diagnosed by the white head with black streaks, a wide black mask and several white spots in the back. Adult *L. kuhli* are distinguished from *L. melanops* by the much darker head (crown almost solidly dark) with a white supercilium and absence of white spots in the back (Brown and Amadon 1968, Thiollay 1994). Immature *L. melanops* have thinner streaks on the head, two white bands in the tail, and inconspicuous brown tips on the feathers of the back and wings (Brown and Amadon 1968, Thiollay 1994, Fergusson-Lees and Christie 2001). The immature plumage of *L. kuhli* has not been fully described. Fergusson-Lees and Christie (2001:621) stated that it is similar to the adult but, apparently, with two or three thin white tail-bands.

The range limits usually accepted for *L. melanops* are northeastern Ecuador and lowland Peru north of the Amazon through southern Colombia and Venezuela, the Guyanas, and Brazil north of the Amazon (Hellmayr and Conover 1949, Amadon 1964, Meyer de Schauensee 1966, Brown and Amadon 1968, Haffer 1987, Sick 1997). *L. kuhli* occurs from lowland eastern Peru south of the Amazon and

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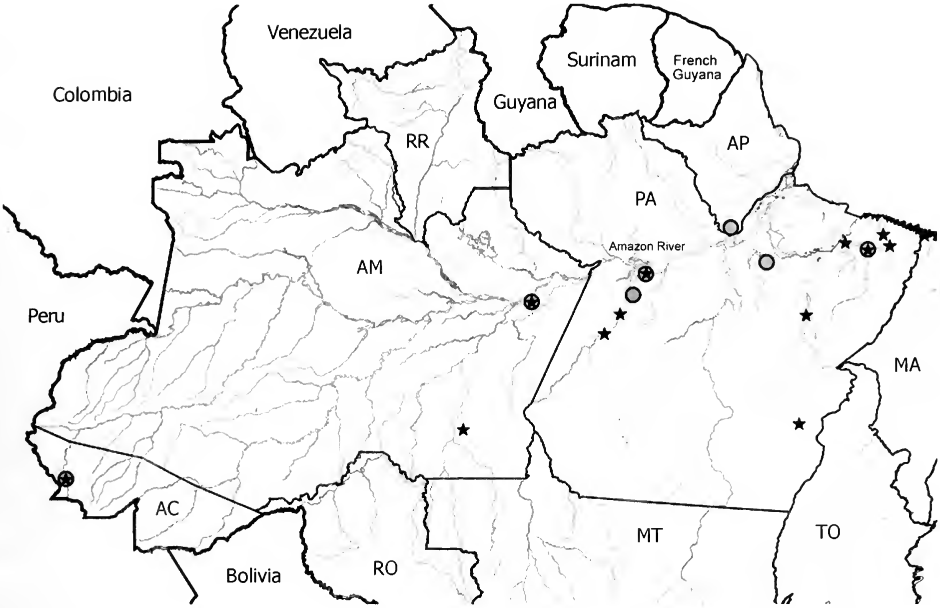

FIG. 1. Distribution of *Leucopternis kuhli* (stars) and *L. melanops* (circles) in Brazilian Amazon, based on plumage patterns of specimens examined by the authors. Localities where the species were sympatric are marked with both symbols. Brazilian states and neighboring South American countries are also indicated.

extreme northern Bolivia through north central Brazil south of the Amazon to eastern Pará (Ferguson-Lees and Christie 2001). Amadon (1964) reported one *L. melanops* collected by A. M. Olalla at Tauarí, lower Tapajós River in 1931 (AMNH 285285). This constituted the first evidence of co-occurrence of *L. melanops* and *L. kuhli* south of the Amazon River. Amadon (1964:9) also referenced a second specimen collected by the Olalla's on the Tapajós River. These records have been considered controversial (e.g., Amadon 1964, Brown and Amadon 1968, Haffer 1987, Thiollay 1994) because of the supposed impossibility of sympatry of such similar species (e.g., Brown and Amadon 1968), or the need for caution due to potential labeling mistakes concerning specimens collected by the Olalla family (e.g., Amadon 1964). Barlow et al. (2002) recently mist-netted and photographed individuals of *L. melanops* and *L. kuhli* on the lower Tapajós River (Fig. 1 in Barlow et al. [2002]), just 6 km apart, documenting sympatry of these species south of the Amazon River.

SPECIMEN EXAMINATION

Examination of plumage patterns of specimens in the collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Paraense Emílio Goeldi (MPEG), and American Museum of Natural History (AMNH) revealed four immature specimens of *L. melanops*, originally identified as *L. kuhli*, collected in at least three different localities south of the Amazon River (Appendix). Two new southern localities are based on Olalla specimens; one an immature male (MZUSP 20360) collected in 1939 at Lago do Batista (= Lago do Baptista), Amazonas, at the same locality where two months later an adult female *L. kuhli* (MZUSP 20359) was collected. The second specimen of *L. melanops* was of unknown gender (MZUSP 46240) collected in 1961 at Santarém, Pará (this could be the second record cited by Amadon [1964], although he did not cite the collection or specimen number of that record). The two remaining specimens were obtained by independent collectors. A male *L. melanops* was collected by Emílio Dente at Capim in 1959 (MZUSP 43863), one month after he collected an adult male *L. kuhli* (MZUSP 43862) at the same locality. The most surprising new southern locality of *L. melanops* is represented by an immature male at MPEG (52705), collected by D. Oren and collaborators in 1996 in the headwaters of the

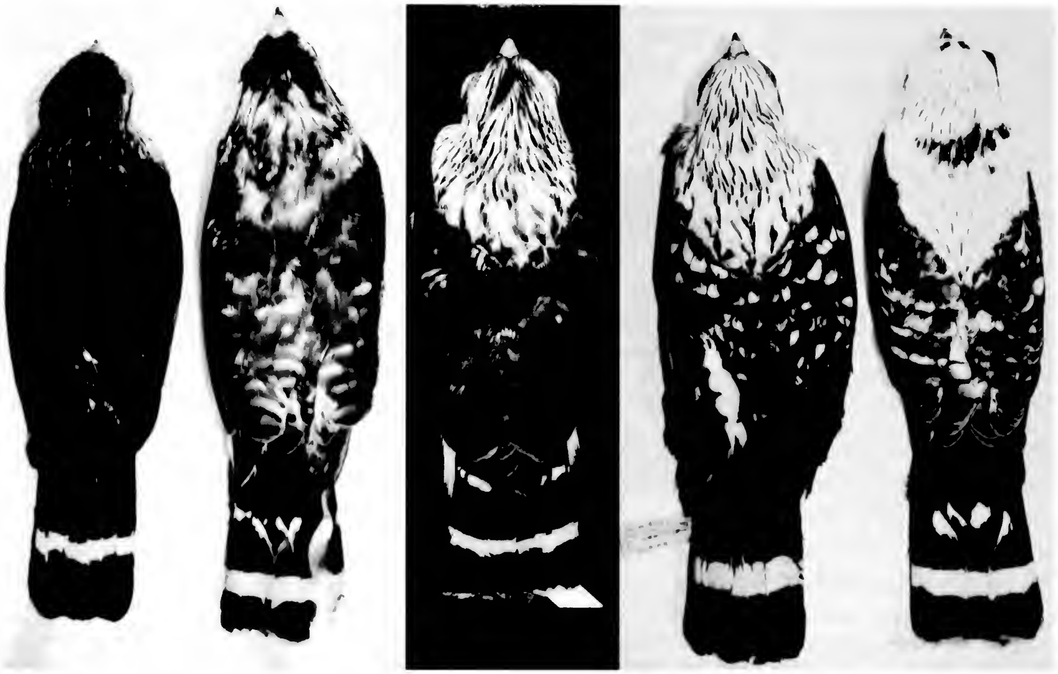

FIG. 2. From left to right: (A) *Leucopternis kuhli*, adult male (MZUSP 43862), immature male (MZUSP 62345); (B) *Leucopternis melanops*, immature male (MPEG 52705, from Acre), adult female (MZUSP 62646), and immature male (MZUSP 43863). Specimens not shown to scale.

Moa River in northwestern Acre, about 1,700 km west of the southernmost record of *L. melanops* (Fig. 1). These new records demonstrate that *L. melanops* occurs in sympatry with *L. kuhli* in the Tapajós River region as well as some other distant localities in southern Amazonia.

The Olalla family collected thousands of birds in South America during the twentieth century. This material is a critically important contribution to Neotropic ornithology not only because of the large number of specimens, but also due to the biogeographic importance of specimens from localities where habitats are currently threatened or have already been destroyed. Critical examination of species distributions based on Olalla material have been generally avoided. The *L. melanops* specimens from Capim and the Moa River, and the observations of Barlow et al. (2002) suggest a concordant pattern of distribution with the specimen from Tauarí and the two other Olalla specimens from southern localities. The aggregation of these independent records, together with the congruence of patterns suggested by Olalla's reptile (P. E. Vanzolini, pers. comm.) and mammal (Mário de Vivo, pers. comm.) collections indicate no evidence of labeling errors in the case of *Leucopternis* hawks.

We found three individuals (MZUSP 10868, 62345, and 72973) among the specimens examined that presented diagnostic characters of *L. kuhli* with the anterior half of the crown almost entirely black, fine black streaks on the sides of the neck, and a white supercilium. These differ considerably from the adult plumage of *L. kuhli* by the presence of numerous white blotches in the back (Fig. 2A), some amount of white in the head and, in the latter two specimens, an inconspicuous second (proximal) white band in the tail. This last character is well documented in the immature plumage of *L. melanops* and *L. semiplumbeus* (Brown and Amadon 1968), two taxa closely allied to *L. kuhli* (Amaral et al. 2006). To our knowledge, this constitutes the only character considered to be indicative of juvenal plumage of *L. kuhli* (Fergusson Lees and Christie 2001). All plumage stages of *L. melanops* have considerably more white in the back, especially the mantle, than any of the three specimens in question (Fig. 2B). We conclude these individuals represent immature *L. kuhli* based only on plumage patterns.

DISCUSSION

Despite recent evidence showing a sister relationship between *L. melanops* and *L. kuhli* (Amaral et al. 2006), population level studies including both species are lacking. It is not possible to assume lack of ongoing gene flow between both species, as well as exclude the possibility of hybrid individuals that could fit the plumage patterns presented here (Fig. 2). Thus, it is necessary to assume (1) there is reciprocal monophyly between *L. melanops* and *L. kuhli*, (2) they represent individual evolutionary units, and (3) the plumage characters used here reflect the independent evolutionary history of both taxa. Furthermore it is possible that even if the species are proven to be independent units, polymorphisms, gender or age linked characters, aberrant plumages or even shared traits may mislead species level identification based only on plumage patterns, Thus, genetic studies at population levels are desirable to test hypotheses of reciprocal monophyly and of possible occurrence of gene flow between the two species, but also to provide further tools to help in identification of specimens. We strongly recommend that tissue samples be saved from all specimens collected and deposited in collections along with voucher specimens to make such studies possible.

We predict that *L. melanops* will be found to occur widely but irregularly in southern Amazonia in *terra firme* forests on sands (tall *campinaranas*) and, perhaps, deeply weathered clays. The four known localities of occurrence are from forests on such soils. The paucity of *L. melanops* specimens from south of the Amazon River may be attributed to an almost complete lack of collecting in *terra firme* forests on sandy soils across that region, and to the close resemblance between this species and *L. kuhli*. Careful examination of specimens in other collections and close attention to the identification of these raptors in the field may increase the known range of *L. melanops* south of the Amazon River. All new records of *L. melanops* in southern Amazonia should be documented with specimens and tissue samples, and if collection is not possible, recordings and photographs accompanied by careful descriptions of plumage. Unfortunately, the primary vocalizations of *L. melanops* and *L. kuhli* (piercing screams that lose amplitude rapidly, usually delivered at intervals of ~3–5 sec for several minutes early in the morning, occasionally given in series of ~4–10 screams at 1–2 sec intervals) are probably not distinguishable in the field. The screams of *L. melanops* tend to be somewhat lower or "heavier" (BMW, pers. obs.). All vocalizing birds should be recorded to help elucidate diagnostic differences with more detailed study in the future. The voice of *L. melanops* south of the Amazon River is presently unknown, but is likely the same as the voice north of the river.

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APPENDIX

Specimens examined (museum number; sex; locality; date; collector; age)

Leucopternis melanops

MZUSP 46240; unsexed; Pará, Santarém; 10 May 1961; Olalla; Immature. MZUSP 20360; ♂; Amazonas, Lago do Baptista; 19 April 1939; Olalla; Immature. MZUSP 43863; ♂; Pará, Capim, BR 14, km 93; 2 October 1959; Dente; Immature. MZUSP 62646; ♀; Amapá, Serra do Navio, Teresinha; 20 February 1965; Santa Brígida; Adult. MPEG 53428; unsexed; Amapá, Fazenda Itapoá; 18 April 1997; Adult. MPEG 47656; unsexed; Amapá, Serra do Navio; 19 October 1965; Instituto Evandro Chagas; Adult. MPEG 17251; unsexed; Amapá, Igarapé Novo; 27 October 1959; M. Moreira; Adult. MPEG 52705; ♂; Acre, alto do Rio Moa; 13 July 1996; D. Oren, B. Whitney, and D. C. Neto; Immature. AMNH 285285; ♀; Tauarí, Rio Tapajós; 19 April 1931; Olalla; Adult.

Leucopternis kuhli

MZUSP 43862; ♂; Pará, Capim, BR 14, km 93; September 1959; Dente; Adult. MZUSP 20359; ♀; Amazonas, Rio Amazonas, Lago do Baptista; 14 June 1939; Olalla; Adult. MZUSP 58120; ♂; Pará, Fordlândia; 11 July 1964; Olalla; Adult. MZUSP 62345; ♂; Amazonas, Margem Oeste do Rio Aripuanã; 22 September 1971; Silva-Filho; Immature. MZUSP 58121; ♀; Pará, Fordlândia; February 1965; Olalla; Adult. MZUSP 10868; ♀; Pará, Rio Tapajós; March 1921; Garbe; Immature. MZUSP 72973; unsexed; unknown locality. MPEG 15734; Pará, rodovia Belém-Brasília km 92; 15 May 1959; Hidasi; Adult. MPEG 32383; unsexed; Pará, Ourém; 28 February 1978; Moreira; Adult. MPEG 32108; unsexed; Pará, Ourém; 10 December 1977; Moreira; Adult. MPEG 22508; unsexed; Pará, Belém (Instituto Agronömico); July 1964; Moreira; Adult. MPEG 23210; unsexed; Pará, Estrada do Coqueiro, Belém; 14 January 1965; Moreira; Adult. MPEG 36684; ♂; Pará, Tucuruí, 10 December 1984; Dente; Adult. MPEG 47658; ♀; Pará, Itaituba; August 1972; Silva; Adult. MPEG 47657; ♀; Pará, Transamazonica, Tapacurazinho; March 1973; Silva; Adult. MPEG 5836; ♀; Pará, Peixe Boi, 29 May 1908; Martins; Adult. MPEG 28112; ♂; Acre, Rio Juruá; 17 July 1956; Moreira; Adult. MPEG 36856; ♂; Maranhão, Carutapera; 12 November 1984; Brigida and Rosemiro; Adult. MPEG 34716; ♀; Pará, Xinguara; 21 February 1983; Adult.

Short Communications

The Wilson Journal of Ornithology 119(3):455–458, 2007

Description of Male Vocalizations of the Turquoise Cotinga (*Cotinga ridgwayi*)

César Sánchez,[1,4] Viviana Ruiz-Gutiérrez,[2] and Daniel Martínez-A.[3]

ABSTRACT.—We describe the first recordings of a male vocalization of the Turquoise Cotinga (*Cotinga ridgwayi*) along with reviewing the sound production in the genus *Cotinga*. Vocalizations were heard in the Coto Brus region of southwestern Costa Rica from late 2003 until early 2005. The vocalization described is different from previous calls known for the species and genus. The vocalization is a pure tone, produced at a high frequency. These vocalizations were observed in a variety of contexts, although more often during alarm or advertisement situations. *Received 18 September 2006. Accepted 14 December 2006.*

The genus *Cotinga* is a monophyletic lineage comprising seven species (Snow 1982, Prum et al. 2000). It is part of one of the least-studied neotropical bird families in which little is known about the ecology and behavior of the majority of species. The *Cotinga* are considered almost voiceless (Snow et al. 2004) but adult males produce mechanical rattling noises during flight (Snow 1982). Until recently, vocalizations had been described only for the Spangled Cotinga (*Cotinga cayana*) (Chaves 2001). Its vocalization is described as a soft, medium-pitched "*hooo*" repeated 2–3 times at irregular intervals, produced while displaying. These displays did not include mechanical sounds emitted during male flights. The other known vocalizations have been produced by females of the genus (Snow et al. 2004). Skutch (1969) observed a female Turquoise Cotinga (*Cotinga ridgwayi*) emitting a clear, monosyllabic "*ic, ic, ic*" alarm-call after its nest was attacked by a toucanet and while searching for the fledgling. The only known male vocalization of the Turquoise Cotinga was heard by F. G. Stiles (pers. comm.) while manipulating a mist-netted bird. The bird emitted a surprisingly loud, mule-like raucous "*caaaoo.*" Here we describe another vocalization uttered by males of the Turquoise Cotinga while adding information on the context of the call production of a Vulnerable and endemic species (Birdlife International 2000). We also provide a general discussion on the sound production of this little known but widespread genus (*Cotinga*).

METHODS

Our observations were from late November 2003 until mid-January 2005. Most observations were made opportunistically while conducting bird-watching tours and every time a cotinga was observed (or heard), we compiled the data. Most of our observations were recorded at Las Cruces Biological Station (LCBS) in southwestern Costa Rica (8° 47′ N, 82° 57′ W), but included observations from Las Alturas Biological Station (8° 57′ N, 82° 50′ W) and other nearby sites. The area surrounding LCBS is a botanical garden that includes a mixture of secondary growth with some emerging canopy trees (Borgella et al. 2001). Turquoise Cotingas varied widely in occurrence during the observation period, ranging from zero individuals for up to 2 months to 2–4 individuals on a daily basis for as long as 30 days. These visits were consistent with high fruit abundance of *Ficus* spp., *Erythroxylum* sp., and species of wild avocados (Lauraceae). Turquoise Cotingas frequently perch on dead exposed branches of trees above canopy level (Stiles and Skutch 1989). Fourteen of 17 observed vocalizations were emitted while cotingas perched high above the ground although, on three occasions, the birds were observed vocalizing below the canopy while feeding as low as 4 m above the ground.

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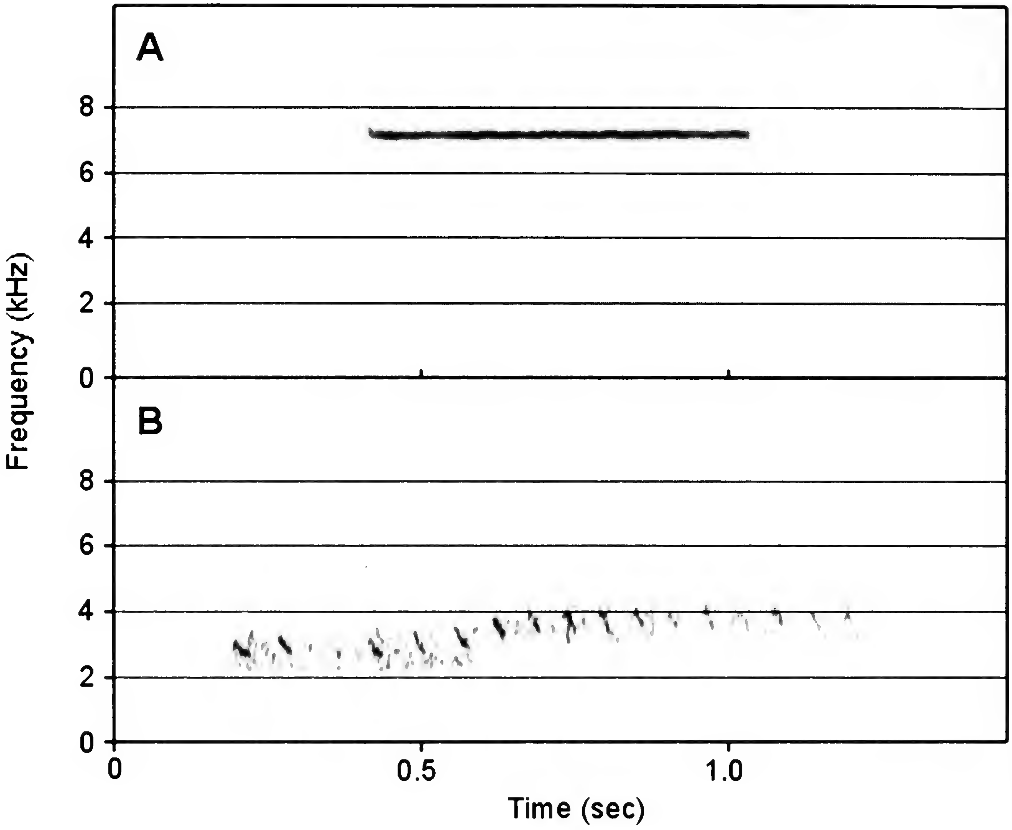

FIG. 1. Vocalization (A) and mechanical sound (B) (produced during flight) of adult male Turquoise Cotingas, Estación Biológica Las Cruces, Puntarenas, Costa Rica.

We were able to make recordings along with our observations of the Turquoise Cotingas. Vocalizations were recorded with a Marantz PMD-222 tape recorder and a Sennheizer MKH-70 microphone. Tapes were deposited at Laboratorio de Bioacústica, Universidad de Costa Rica. Sounds were digitized with Raven 1.2.1 (Charif et al. 2004) at 44100 Hz (16 bit). We used this software to measure and analyze the sonograms following these settings: transform length = 512 points, frequency resolution = 86.1 Hz, time resolution = 1.18 msec, and window = hamming.

OBSERVATIONS

We observed males uttering vocalizations during 15 occasions at LCBS and two occasions at Las Alturas. Some individuals were observed opening their bills wide while emitting the vocalization. The vocalization is a pure tone, resembling a metallic high pitch, with almost no frequency modulation (Fig. 1A). Two songs were recorded on 21 July 2004, although we were not able to detect whether they were emitted by the same male or by two individuals. Both vocalizations are similar and the variables measured confirm their resemblance: high frequency = 7.33 and 7.30 kHz, respectively; low frequency = 7.06 and 7.02 kHz; frequency range = 0.27 and 0.28 kHz; song length = 0.59 and 0.62 sec; maximum frequency = 7.17 and 7.14 kHz; maximum power = 97 and 82.7 decibels. The different distances from the birds to the microphone (4 and 25 m) largely explains the difference in maximum power. The first vocalization occurred when a male flew directly towards another, which was perched and feeding. When the approaching male was close to the perched male, it vocalized and proceeded to move within the same tree. The second vocalization was recorded while one male was feeding, but we were not able to see the individual at the moment it vocalized.

We also heard but did not record this same type of vocalization on 15 occasions. During two observations, adult males vocalized after interacting with individuals of the same or other species. One occurred when an immature male flew towards an adult perched male, landing within 2 m. The adult vocalized once as soon as the immature male landed. Another non-recorded vocalization was produced when a male, perched at the top of a ~25 m tall tree, was approached by two flying Brown-hooded Parrots (*Pionopsitta haematotis*), which landed within a meter. The cotinga vocalized when the parrots landed, but afterwards the bird remained in the tree for at least 10 min without vocalizing. Other observations occurred—seemingly—without interactions with other birds. On two consecutive occasions, we heard an individual emit a series of three vocalizations every 20–30 sec. Another individual produced one vocalization three times about every 2 min. Males were observed emitting the same vocalization in three other occasions, but no apparent interactions were noticed with other individuals from the same or other species. Several interactions (e.g., harassments, fly-overs) were observed between males, females, and both genders without vocalizations being emitted. All vocalizations observed were produced by adult males; we observed females or young males on eight occasions but they did not vocalize.

The other sounds known for male Turquoise Cotingas are mechanical "rattles," produced during flight (Fig. 1B). Each time a male flies, it produces a stuttering or tittering sound, even when making short sallies (>1 m) (CS, pers. obs.). These sounds are a series of short pulses, which start at low frequencies and increase in frequency and bandwidth until leveling off at the fourth or fifth pulse. The length of each pulse is variable and the number of pulses depends on the length of the distance traveled by the bird. We speculate these sounds are produced by the modified 9th and 10th primaries. These feathers are thinner than the rest of the primaries, and slightly bent at the tip, with P 9 measuring about half the width of P 10 (P 9 = 2.3 mm, P 10 = 4.45 mm, measured at 10 mm from the tip, $n = 1$, UCR # 1481). The mechanics of sound production with wing feathers have not been studied for Turquoise Cotinga or any other species in the genus to our knowledge.

DISCUSSION

Our observations indicate that male Turquoise Cotinga not only produce vocal sounds, but they also produce them fairly regularly. The vocalization was only seen produced by adult males, despite several months of observations, and not by females or young males. The predominance of male vocalization in the Cotingidae is a common phenomenon, a trait often considered to be sexually selected (Andersson 1994). This is consistent with the high extent of sexual dimorphism present in most members of the family, including the genus *Cotinga*. Kroodsma (2004) recently suggested that some members of the Cotingidae can learn their songs. Young Three-wattled Bellbirds (*Procnias tricarunculatus*) take 6–7 years to perfect their dialects and it can be expected that other members in the family can take several years to perform their adult vocalizations. This might explain why no young male Turquoise Cotingas were observed vocalizing.

The vocalization seems to serve as an advertisement or as an alarm, as it was produced during encounters with individuals approaching the calling male. Other vocalizations heard occurred during events where we did not record interactions between members of the same or other species. It is possible the vocalization occurs in another context rather than advertisement-alarm. Our observations span more than a year suggesting cotingas do not emit calls only during the breeding season as Turquoise Cotingas are known to breed during March (Stiles and Skutch 1989).

The function of mechanical sounds produced with the wings remains untested but probably is related to sexual displays and mate attraction (Snow 1982). We suggest this because: (1) modified feathers are only found in males of this highly dimorphic genus, (2) modifications of feathers are known to occur in species that produce mechanical sounds (which are mainly used during courtship) (Stettenheim 1976, Prum 1998), and (3) a sister clade, Pipridae (Prum and Lanyon 1989) also exhibits sexual dimorphism, and males produce mechanical sounds with modified feathers during courtship (Snow 2004). Our observations indicate that male Turquoise Cotingas produce at least three different sounds used in different contexts. The available information shows the importance of vocalizations in a genus that until recently was considered almost voiceless (Snow et al. 2004). More detailed observations should show whether Spangled and Turquoise cotingas are the only species of *Cotinga* that vocalize.

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Nesting Behavior and Nestling Care of the Pavonine Quetzal (*Pharomachrus pavoninus*)

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ABSTRACT.—I describe the nesting behavior of the Pavonine Quetzal (*Pharomachrus pavoninus*) at Los Amigos in the southeastern Peruvian Amazon. I found a single nest cavity 4.2 m above ground in a dead snag in *terra firme* forest. The cavity contained two pale blue eggs each with a few small brown-buff speckles, of which one hatched. I observed incubation between 18 February and 2 March 2004. Based on an average of 0.7 observation hrs/day, the male appeared to incubate during most of the day from at least 0950 hrs until sunset (near 1745 hrs) when the pair would switch before nightfall. The female appeared to incubate at night and during the early morning. Fifty-six percent of 32 food deliveries observed between 6 and 26 March were tree frogs and 44% were fruits. The

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nestling fledged on 26 March, 20 days after the first observed food provisioning. The nestling period is estimated to be 21–24 days. The plumage development of the nestling, vocalizations, and other observations are discussed and compared with the Resplendent Quetzal (*Pharomachrus mocinno*). *Received 2 October 2006. Accepted 28 December 2006.*

The Pavonine Quetzal (*Pharomachrus pavoninus*) is widespread in the Amazon, but little is known about its natural history. One probable nest of this species was reported 9 m above ground in a large tree during February in Brazil (Oriki and Willis 1983, *in* Johnsgard 2000). There is an unreferenced mention in Collar (2001) of a full grown nestling seen in a hollow 5 m above ground in a dead tree on 19 July 2000 along the Río Sucusari, Loreto, Peru (Josep del Hoyo, pers. comm.). The diets of other trogons are known to include a mixture of animals and fruit, but *Pharomachrus* quetzals are thought to be almost entirely frugivorous (Remsen et al. 1993, Collar 2001), specializing on Lauraceous fruits and serving as important seed dispersers (Avila et al. 1996). Remsen et al. (1993) examined nine Pavonine Quetzal stomachs and found eight to contain only fruit and one to contain fruit and arthropods. The Resplendent Quetzal (*P. mocinno*) is known to feed its nestlings fruit, arthropods, and vertebrates (Skutch 1944, Wheelwright 1983, Avila et al. 1996).

Here I report observations of a Pavonine Quetzal nest, including descriptions of the nest cavity, eggs, incubation behavior, and food provisioning during February and March 2004 in southeast Peru. I also discuss the plumage development of the nestling, vocalizations, and other observations and compare the nesting behavior and food-provisioning to that of the better known Resplendent Quetzal.

METHODS

I discovered the Pavonine Quetzal nest near the Centro de Investigación y Capacitación Río Los Amigos (CICRA), Depto. Madre de Dios, Peru. CICRA is at an elevation of 250 m above sea level, along the north bank of the Río Madre de Dios near the mouth of the Río Los Amigos (12° 34′ S, 70° 05′ W). The lowland tropical forests and climate of CICRA are similar to that of other, better known field stations in the region within Manu and Tambopata National parks. More information on climate, geology, vegetation, and trails at CICRA is available at www.amazonconservation.org/home and in Pitman (2006).

I monitored the quetzal nest most days during the rainy season between discovery on 18 February and fledging of the single nestling on 26 March 2004. I spent ≥6.3 hrs observing the nest during incubation over 9 days between 18 February and 2 March (mean = 0.7 hrs/day) and ≥40.3 hrs when adults provisioned food to the nest over 14 days between 6 and 26 March (mean = 2.9 hrs/day). I constructed a blind 12 m uphill from the nest tree using a small tent to observe adults switch incubation duties at the nest at sunset (1413–1800 hrs on 21 Feb, 1655–1750 hrs on 23 Feb, 1711–1756 hrs on 24 Feb) and, to minimize disturbance. I examined the nest and eggs directly on 22 February using a ladder to access, photograph, and measure the nest and eggs, spending less than 20 min near the nest to minimize disturbance.

I sat quietly in the open to observe food provisioning because of limited visibility inside the tent. Adults arrived with food and approached to within 2 m of the nest cavity, but appeared wary of entering while I was nearby. I identified delivered food items as fruit or animal, described them in my notes, and left the nest site for 20–40 min to allow the adult to feed the young. I accessed the nest again on 15 March by ladder to count nestlings and to collect regurgitated seeds. I also collected regurgitated seeds from the nest cavity on 27 March after the nestling fledged. Seeds were identified by Fernando Cornejo Valverde (Botanical Research Institute of Texas). I identified frogs using photographs accompanying Cocroft et al. (2001).

RESULTS

The nest cavity was in a large dead tree trunk on a hillside in *terra firme* forest at an elevation of 205 m above sea level (12° 33′ S, 70° 07′ W). The tree snag was 7–8 m tall, rotting with multiple cavities, small buttresses at the base, and a circumference at breast height of 0.85 m. The nest was in a cavity on the western and uphill side of the snag 4.2 m above ground. The nest entrance was circular with a large wedge-shaped opening descend-

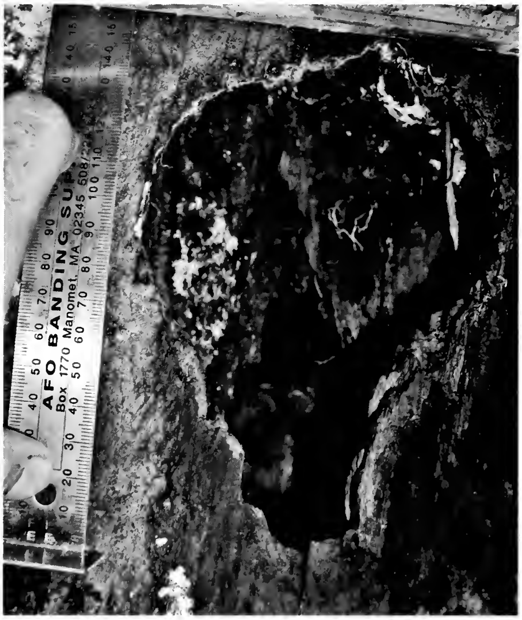

FIG 1. Nest entrance of the Pavonine Quetzel (note ruler [mm] for scale).

ing from the bottom of the entrance (Fig. 1). The circular portion was 9 cm high by 11 cm wide and the wedge-shaped opening below was 7 cm wide and descended 6 cm downwards. The cavity was 16 cm wide and 21 cm deep from the base of the entrance. The cavity appeared shallow, but both adults fit inside without a single feather visible from outside. I observed no lining in the nest, but the bottom contained soft bits of rotten wood.

The nest contained two eggs on 22 February, each pale blue with a few small brown-buff speckles and warm to the touch. The first egg was 31.5 mm long × 27.6 mm wide and weighed 8.5 g. The second egg was 32.4 mm long × 28.1 mm wide and 13.5 g. The second egg failed to hatch and was rotten when I examined the nest on 15 March. I removed it from the nest and prepared it as a specimen for the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos in Lima, Peru.

I observed the male incubating during the daytime (0950–1015 hrs, 22 Feb; 1210 hrs, 27 Feb; 1241–1304 hrs, 20 Feb; 1300 hrs, 18 Feb; 1413–1744 hrs, 21 Feb; 1530 hrs, 19 Feb; 1655–1717 hrs, 23 Feb) between 18 February and 2 March from at least 0950 hrs until sunset near 1745 hrs when the pair would switch. The female appeared to incubate at night and during the early morning (0650 hrs, 2 Mar). Incubation appeared to last ≥14–17 days, but is not known because I likely discovered the nest after eggs had already been laid.

I observed the adults deliver 32 food items to the nest between 6 and 26 March. The male (25 of 32 food deliveries) seemed to provision the nestling more often than the female, especially near time of fledging. I observed the male deliver food on 16 occasions and the female deliver food once from 22 to 26 March. On 25 March, I observed the male bring food to the nestling 10 times while the female delivered no food. Frog deliveries tended to be alternated with fruit deliveries and the type of fruit (based on color and size) seemed to be alternated between fruit deliveries so that no single food item was repeatedly delivered in three consecutive observed deliveries.

Tree frogs were the most-frequently delivered food item and no insects, lizards or other animal prey were observed delivered to the nest. Eighteen (56%, $n = 32$) of the food deliveries observed were tree frogs and the remaining 14 (44%, $n = 32$) were fruits. Between 6 and 15 March, 66% (10 of 15 food items) of food brought to the nest were frogs. After 21 March, the percentage of fruit brought to the nest increased to 53% (9 of 17 food items), but frogs were still delivered through the nestling's last full day at the nest. Fruits brought to the nest varied in color (black, green, red) and in size, but were difficult to identify by sight. All tree frogs appeared to belong to the genera *Hyla* and *Phyllomedusa*.

Seeds ($n = 31$) regurgitated by the nestling were collected from within and directly below the nest. These were predominantly (52%, $n = 16$) Lauraceae seeds of various sizes, but also included six *Euterpe precatoria* (Arecaceae) seeds, four *Iryanthera* sp. (Myristicaceae) seeds, one unidentified seed, and one seed of each of *Pouteria* sp. (Sapotaceae), *Guatteria* sp. (Annonaceae), and *Unonopsis* sp. (Annonaceae). A seed capsule fragment of *Tetragastris* sp. (Buceraceae) also was found on the ground beneath the nest.

I observed the single nestling on 15 March at 10–13 days of age (Fig. 2), sitting in the

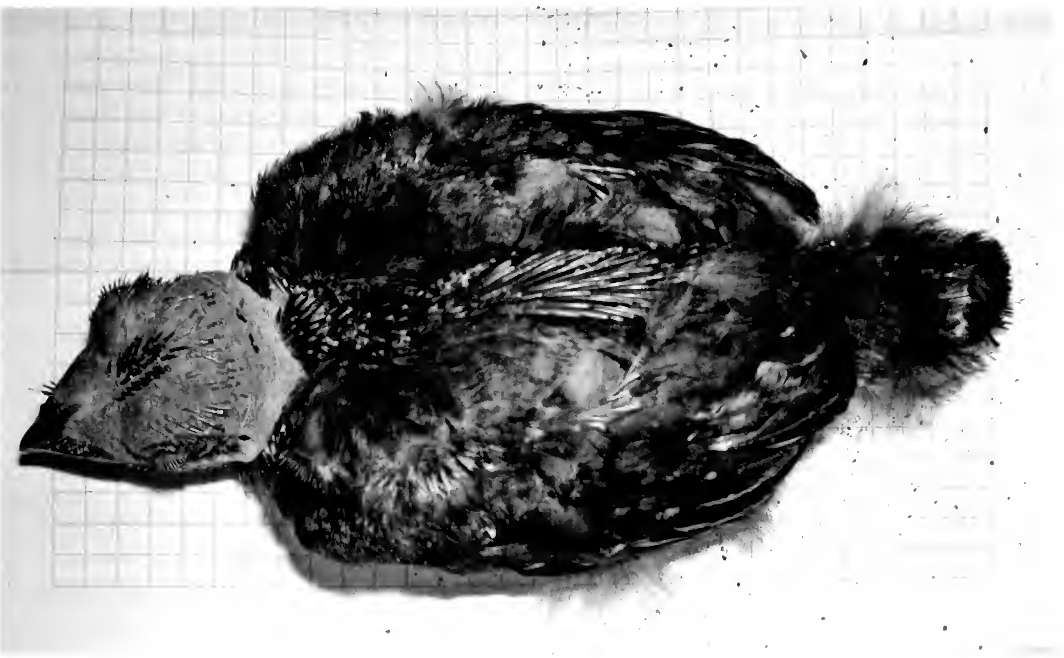

FIG. 2. Dorsal view of nestling Pavonine Quetzel (on 0.5 cm grid paper), 15 March 2004.

nest with its head propped against the cavity wall and its beak pointing up towards the cavity entrance. The nestling was weighed (103 g) and described: bill black with pale tip; legs and feet gray with flesh colored pads; eyes dark; plumage lacking from most of head and belly below sternum, skin gray; breast covered in soft tawny feathers tipped buff to give a somewhat mottled appearance; short black feathers surrounded the cloaca; downy undertail coverts tawny; pin feathers protruded from skin on crown and back; scapulars blackish, edged rufous to golden green; lesser coverts blackish tipped brown, greater coverts blackish tipped buff, remiges blackish with buff margins; upper tail coverts dusky; remiges blackish, new and short, with outer remiges possibly emerging with white tips.

The nestling fledged on 26 March, 21 days after the first observed food provisioning. The nestling period is estimated to be between 21 and 24 days. The nestling spent ≥5 hrs peering out of the entrance on 25 March, at times leaning out to look in the direction of the male, and other times calling softly. I heard the nestling give a soft "ow," and at other times I heard the male call "Eeeooow tuk" and the female give a soft "Wa op-op-op-op-op" chuckle (possibly in alarm).

The nestling peered out of the entrance while the male was not nearby and appeared undisturbed by my activities or other researchers on a nearby trail. On three occasions I observed it lift its wings within the entrance and preen once. On five occasions the male sallied to the nest and returned to a nearby perch without delivering the food item in its beak to the nestling. At times the male called, possibly urging the nestling to follow. Upon my arrival at 0747 hrs on 26 March, I found the nestling peering from the entrance with the male perched 2 m distant holding a small green fruit in its beak. At 0755 hrs the male sallied to the entrance and returned to the perch with the fruit still in its beak. Soon after, the nestling flew ~30 m to the south, immediately followed by the male. I observed the male again 50 m to the south of the nest with nothing in its beak, but it soon regurgitated a small green fruit. I spotted the fledgling awkwardly land on a branch about 14 m above ground in the forest midstory after what presumably was a short second flight. The male quickly flew and perched on a nearby branch underneath the fledgling. Both birds then moved south out of view.

At fledging, most of the fledgling's head was covered by short gray plumage, with a few pin feathers still coming in on the forecrown. The skin around its eyes, lores, and throat appeared bare. Its back and upper breast plumage was green, bordered by mottled tawny plumage on the remainder of the breast and belly. The wings were blackish with buff spots on the coverts and buff margins on the remiges. The short retrices were black, with a short whitish tip visible on the right outer retrix.

The adult female had a dark gray bill (not red as sometimes illustrated). Overall the female's plumage was: head brownish gray (rather than green as sometimes illustrated), bordered by a band of emerald around the upper breast, neck and back; mid-breast brownish gray like the head, contrasting with ruby lower belly; undersides of retrices black with thin white bands on lower half of outer web, one white band on inner web, and thin white terminal band.

DISCUSSION

This paper reports the first measurements of the nest cavity and description of eggs, nestling, and food provisioning for the Pavonine Quetzal. The timing of breeding at this nest in southeastern Peru (Feb–Mar) was different from Loreto (mid-Jul, Collar 2001). January, February, and March at CICRA are on average the three wettest months of the year (CICRA 2004), whereas July is relatively dry in Loreto (Marengo 1998). Data from additional nests across the range of this species are necessary to investigate how rainfall or seasonality may influence timing of breeding, but it is interesting these two nests were found during such different seasons (dry vs. wet).

The nest, clutch, egg color, nestling plumage, and nestling posture of the Pavonine Quetzal appear similar to that of Resplendent Quetzals (Skutch 1944, Johnsgard 2000). The male Pavonine Quetzal's plumage became quite worn by the time the nestling fledged, as occurs in Resplendant Quetzals (Skutch 1944). Frogs, rather than other animals, accounted for 56% of food deliveries to the Pavonine Quetzal nestling, more than delivered to Resplendent Quetzal nests in Mexico (25.9% arthropods, 4.9% reptiles, 0.6% amphibians; Avila et al. 1996) and Costa Rica (61.7% arthropods, 4.1% snails, 4.6% reptiles, no amphibians; Wheelwright 1983). No frogs were recorded among food items delivered to a Golden-headed Quetzal (*Pharomachrus auriceps*) nest in Ecuador (R. G. Lohnes, pers. comm.).

The Pavonine Quetzal nestling was provisioned with a higher percentage of fruit (33%) during the first 10 days of observation than Resplendent Quetzal nestlings in Mexico (24%; Avila et al. 1996) and Costa Rica (21%; Wheelwright 1983). The Pavonine Quetzal nestling was provisioned with 53% fruits after the first 10 days of development, lower than Resplendent Quetzal nestlings in Mexico (72%; Avila et al. 1996), but higher than nestlings in Costa Rica (34%; Wheelwright 1983). These differences could reflect different food availabilities or diet requirements between quetzal populations or may be due to small sample sizes (one nest here and in Avila et al. 1996, 11 nests in Wheelwright 1983). Lauraceae seeds represented 52% of the seeds recovered from the Pavonine Quetzal nest and comprised 50% of the total fruit items in the diet of the Resplendent Quetzal in Mexico (Avila et al. 1996). The observed nestling period of 21–24 days for this nest was similar to that of Resplendent Quetzals (21–23 days in Costa Rica, Skutch 1944, Wheelwright 1983; 27 days in Mexico, Avila et al. 1996). Conclusions from this and other studies of quetzal nests based on small samples are difficult, and further research could reveal more variation over multiple nests, years, and locations in timing of breeding, incubation patterns, and food items provisioned.

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Mating Behavior of Reed Buntings (*Emberiza schoeniclus*) in Captivity

Katja Wingelmaier,[1,2,3] Hans Winkler,[1] and Erwin Nemeth[1]

ABSTRACT.—We studied sexual pair behavior and cuckoldry of nine female and five male Reed Buntings (*Emberiza schoeniclus*) in a large outdoor aviary. Three males established small territories and paired with females. We observed 23 copulation attempts with identified partners during a period of approximately 6 weeks, 10 between social mates, 12 between unpaired females and paired males (extrapair for males), and one between a paired female and a paired male which was not the social mate (extrapair for both). Both males and females initiated copulation attempts which, in most cases, were preceded by precopulatory displays. No forced copulations were observed and females appeared to have an active role in mating behavior. *Received 2 October 2006. Accepted 15 December 2006.*

Paternity analyses have revealed the majority of socially monogamous birds are genetically promiscuous (e.g., Birkhead and Møller 1992, Westneat and Stewart 2003). Surprisingly little is known about the actual mating behavior in contrast to a flood of genetic data. Detailed knowledge of events that lead to copulations is crucial for deciding whether extrapair behavior is male or female-driven, or both (Westneat and Stewart 2003). Observations of extrapair copulations in the field are scarce and studies of birds in captivity may yield more data on this behavior. The rate of extrapair paternity (EPP) in the Reed Bunting (*Emberiza schoeniclus*) is one of the highest reported in socially monogamous birds (Westneat and Stewart 2003). It ranges from 30 to 55% of the young (Dixon 1993, Buchanan 2001, Kleven and Lifjeld 2005, Bouwman et al. 2006; EN, unpubl. data). However, observations of extrapair copulations (EPCs) in this species are rare (Bouwman et al. 2006); to our knowledge there are no published data on which partner initiates copulations. Marthin-

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sen et al. (2005) observed intrusions of extrapair males into female territories. That suggests that males intend to initiate EPCs, but it is not known how the female reacts to these intrusions and whether she intrudes into extrapair male territories (Kleven et al. 2006). The objective of our study is to provide detailed descriptions of copulatory behavior in the Reed Bunting with social mates as well as with extrapair partners. We investigated this behavior in a large outdoor aviary where males and females had access to different mating partners.

METHODS

Fourteen Reed Buntings (9 females, 5 males) were studied in captivity from mid-June to late July 2005 at the Konrad Lorenz Institute in Vienna, Austria. They had been caught one and one-half year before observations started. The color-ringed birds were kept together with 10 Bearded Tits (*Panurus biarmicus*) in an outdoor aviary. The aviary was 78.8 m^2 in area and consisted of 14 interconnected rectangular compartments (3 × 1.88 m). The maximal height was 3.20 m. Each compartment contained pots with sedges and dead reed stems, willow (*Salix* spp.) branches, and bamboo (*Phyllostachys aurea*). Pine (*Pinus* spp.) twigs were attached to the walls because they have been demonstrated to be used as nest sites by captive Reed Buntings (Giebing 1995). All nests except one were built in small wicker baskets, 5 cm in diameter, mounted with wire on reed stems or pine twigs at a height of 0.5–1.8 m. Sufficient nesting material (dog and horse hair, dried grass) was placed in each compartment. We provided *ad libitum* mealworms, ant pupae, crickets, and soft food with various seeds, insects, and mussels. Territory sizes ranged from one to six compartments and each territory had at least one feeding place. The entire aviary was divided between territorial males and there were no neutral or common feeding grounds. Three of the five males were paired.

Pairs or individuals were observed for 1–3 hrs (all pairs in 40 hrs total) between 0800 and 1800 hrs CET. Either the male's social mate or a female in the territorial neighborhood was fertile during observation. We ascertained social pairs by mate guarding and the male's participation in incubation or feeding of young. We recorded the distance between pair members every 2 min similar to Marthinsen et al. (2005) to investigate mate guarding. The male followed his mate in close proximity, more or less constantly, in this period. We defined the time a male spent within 3 m of the mate as time spent mate guarding. Mate guarding was clearly distinguishable from periods without mate guarding when males showed little interest in their mates. Unpaired females were not mate-guarded or relegated to one territory. We scored copulations of these females with paired males as EPCs for males. We classified copulation attempts as male or female initiated when we were able to observe precopulatory behavior. We scored copulation attempts as female initiated if the female approached the male first or showed a soliciting display. All other cases were classified as male initiated.

OBSERVATIONS

Males sang and defended their established territories and, after pair formation, females started building nests. Twenty-five of 28 broods failed due to predation. We could not ascertain the type of predators responsible but the most likely candidates were mice (*Mus musculus*, *Apodemus* spp.), snakes (Colubridae), and weasels (*Mustela* spp.). We assume they gained access to nests through small gaps and holes in the aviary. Only 11 chicks fledged from the three successful nests from May to July.

Three of the five males in the aviary mate guarded their females 36 to 100% of the observed time (8 observation sessions). The earliest mate guarding observed was 7 days before egg-laying. Mate guarding did not occur after the day the second egg of the clutch was laid.

Copulation attempts (n = 25) occurred between day 4 of the pre-egg-laying phase and day 2 after the first egg. All but one occurred on the ground. We observed 17 successful and eight failed copulation attempts (Table 1) within 9–11 different pairs. Only three of these pairs were social pairs (10 copulation attempts). Six females and 3–5 males were involved in all attempts; in two cases male identity could not be ascertained. Within pairs, unsuccessful attempts failed because females rejected males. EPCs of paired males with un-

TABLE 1. Copulation attempts of captive Reed Buntings (within-pair [WP], extrapair [EP], with unidentified males [?]).

	Failed	Successful	Initiation by male	Initiation by female	Initiation unknown
WP	2	8	1	3	6
EP paired males - unpaired females	3	9	3	4	5
EP paired males - paired females	1				1
? Unidentified males - unpaired females	2		1	1	

paired females failed because females rejected males (n = 2) or the attempt was interrupted by the social female (n = 1). We observed one unsuccessful EPC attempt between a paired male and a paired female, which were not social partners. It failed, because an unidentified male interfered. The two additional unsuccessful copulation attempts with unpaired females and unidentified males failed because females rejected the attempts.

We were able to observe the behavior preceding copulations in only 13 of 25 mating attempts. Copulations occurred on two of these 13 occasions without any preceding displays. In all other cases precopulatory behavior consisted of more or less complex interactions between males and females. Our observations showed that both males and females initiated copulation attempts (Table 1). Males showed a complex precopulatory courtship display (the ‘fluffed-run’ [Andrew 1957]) in 77% (10/13) of the cases. The fluffed run occurred in open spaces on the ground when males made a series of swift runs towards or in a circle around the female with a more or less vertical, sometimes erect body, bent legs, ruffled feathers on rump and head, the bill occasionally lowered, trailed wings, and a spread and drooped tail. Before mounting, males approached females from behind and hovered over them, standing with flapping wings, looking down, and then attempted to copulate. The bodies of the females during copulation were horizontal, the tails erect, so that cloacae could come in contact. The males flew some distance (0.5–1.5 m) after copulating for approximately 3–4 sec. Males started the fluffed run either before females were approaching them (4/10) or when females were already nearby (6/10). Females approached singing males three times. On two of these occasions, males ceased singing and started the fluffed run; in one case the male continued to sing at low volume during the fluffed run. These were the only observations where male song preceded a mating attempt. Males performing a fluffed run were attacked by neighboring males at least three times. In one copulation attempt a female displayed a fluffed run in reaction to the mate’s fluffed run.

We found high plasticity in female behavior connected to copulations. Both paired and unpaired females approached displaying or nondisplaying males (8/13) to initiate copulations (Table 1). On two occasions, females rejected copulation attempts by a bill forward gesture towards the males, which already hovered over them. In one case the rejected male was the social partner. One unpaired female gave the female soliciting display (Andrew 1957) twice when a male was nearby. In this display, the female crouched with her body in a horizontal posture and the bill, head, and tail were raised while she rapidly quivered her raised wings. We did not observe a female performing this soliciting display in reaction to the male’s courtship run.

We observed male post-copulatory behavior on one occasion when a male became prostrate on the ground with the bill pointing upwards. When the male gave this display, the female mounted, and the male disengaged himself by walking forward.

DISCUSSION

Mating was often initiated with displays described by Andrew (1957). Copulations occurred on only two occasions without any preceding displays. Precopulatory interactions were a complex behavioral chain consisting of male and female displays to demonstrate the inclination to copulate. Reed Bunting males, in contrast to three other Emberizinae species (Andrew 1957), often displayed with an erect head. In this position their black badge, which extends from their submoustachial white stripe to the upper breast, was clearly visible. Badge color was correlated with fertilization success in a Dutch population (Bouwman et al. 2006). The fluffed run could have developed to present the male's plumage features provided that females choose between males. One male sang during his fluffed run on one occasion, indicating that song might also be an indicator of male quality as shown by Bouwman et al. (2006).

We observed a male post-copulatory behavior which had only been reported once for the Reed Bunting (Andrew 1957), but which is common in the Yellow-breasted Bunting (*Emberiza aureola*). This was the prone-display ('head-up-lie-flat') (Masatomi and Kobayashi 1982) which resembles the female's soliciting display. The female reaction to the male prone-display was mounting in the Reed Bunting as well as in the Yellow-breasted Bunting. Male post-copulatory and reversed sexual displays have been described for other Emberizinae species (Andrew 1957) and are known in passerine and non-passerine species (e.g., Lorenz 1941, Nero 1982). The function of this display is enigmatic in the Reed Bunting as it is in other species. It possibly may have a role in pair bond maintenance or signaling a successful copulation (Johnson et al. 2000).

Males spent a considerable amount of time mate guarding and ceased guarding after the second egg was laid as reported by Marthinsen et al. (2005). The frequency of copulation attempts was probably influenced by the specific situations in the aviary. Thirteen of 25 copulation attempts were extrapair for males and we observed only one paired female copulating with an extrapair male. Our results are probably not directly applicable to field conditions due to the female biased sex ratio and good mate guarding conditions in the aviary. However, our observations reveal that females actively engage in sexual behavior and we are not convinced that females behave completely different in the field. No copulation appeared to be forced by the male. In both within-pair and extrapair copulation attempts, females could show their willingness for copulation by approaching the male and were able to reject copulations. It seems doubtful that females have a passive role in cuckoldry as proposed by Marthinsen et al. (2005). We expect that female Reed Buntings are able to selectively accept and reject EPCs in the field.

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Nesting Home Range and Movements of an Urban White-winged Dove Population

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ABSTRACT.—We monitored nesting home ranges of White-winged Doves (*Zenaida asiatica*) in Waco, Texas using field-implanted, subcutaneous radio transmitters. Mean nesting home-range size differed by gender (75.7 km^2 for females, 31.9 km^2 for males, $P = 0.17$). Mean nesting home-range for all individuals of known gender differed by year (75.6 km^2 for 2002, 32.0 km^2 for 2003, $P < 0.001$). Within-year mean nesting home ranges for individuals differed by gender for 2002 but did not for 2003. We received reports of 35 band recoveries (2.3% of those banded) through March 2004. Distance moved did not differ by year, gender for adults, or for gender by age. Distances of recoveries from banding sites ranged from 0 to 477.4 km. *Received 24 October 2005. Accepted 30 October 2006.*

The historical northern extent of the range of White-winged Doves (*Zenaida asiatica*) in the United States has been restricted to the southern, semi-arid portions of Texas, New Mexico, Arizona, and California (George et al. 1994). The largest population occurred in the Lower Rio Grande Valley (LRGV) of Texas, a four-county region at the southern-most portion of the state in the Tamaulipian biotic province (Blair 1950, Hayslette et al. 1996). White-winged Doves in Texas have been expanding their range northward since about 1950, forming large, urban populations consisting of some resident individuals (Small et al. 1989, Hayslette and Hayslette 1999). Currently, it is not known what proportion of the peak breeding population over-winters, but preliminary indications are that it is about one-third (MFS, pers. obs.). These urban populations of White-winged Doves have grown substantially in the last 35 years in Texas, while populations in the LRGV have become more urbanized and less migratory (Small and Waggerman 1999).

Habitat degradation in the LRGV (Curtis and Ripley 1975; Lonard and Judd 1985, 1991; Brush and Cantu 1998) coupled with anthropogenic landscape scale changes increasing habitat suitability north of the LRGV may be facilitating this change in White-winged Dove distribution (Kiel and Harris 1956, Cottam and Trefethen 1968, West et al. 1993). White-winged Doves in Texas have demonstrated a dramatic shift in distribution over a relatively short period of time. Thus, quantification of breeding ecology and movement is necessary for evaluating the current status of populations in Texas.

The objectives of our study were to: (1) document nesting home range and (2) non-migratory movements of White-winged Doves, based on band recoveries, for a recently colonized urban population.

METHODS

We conducted our study in Waco, Texas (McLennan County), primarily because of its relatively recent colonization by White-winged Doves (Schaefer 2004). We trapped 1,517 White-winged Doves using standard walk-in funnel traps (Reeves et al. 1968) baited with a 2:1 ratio of cracked corn (*Zea mays*) and black-oil sunflower (*Helianthus annulus*) seeds from 16 January to 17 June 2002 and 20 January to 11 July 2003. All White-winged Doves were banded with federal aluminum leg bands prior to release and age, trap location, and gender (when possible) were recorded. Age was categorized as adult (AHY) or hatching year (HY). Gender of adults in 2002 was based on cloacal characters (Miller and Wagner 1955, Swanson and Rappole 1992).

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Doves banded in 2003 were not identified to gender. Gender of radio-marked birds in 2003 was assigned primarily by when (time of day) the marked individual was observed on a nest. Males typically care for eggs and hatchlings the majority of the day and females are on the nest at night (Cottam and Trefethen 1968).

We surgically implanted subcutaneous radio-transmitters (Advanced Telemetry Systems, Isanti, MN, USA) (Schulz et al. 1998, 2001; Small et al. 2004a) in 79 White-winged Doves (13–17 Jun 2002: 16 males, 23 females; 19 Feb–11 Mar 2003: 17 males, 17 females, 6 unknown) using a portable anesthesia unit (Small et al. 2004b). We performed surgeries at the trap site to reduce the impact on nesting behavior. We released birds when they regained a lucid state, usually <20 min post-surgery. All methods for handling doves were approved by Texas State University–San Marcos' Animal Care and Use Committee (protocol number 5QEKCT).

Transmitters weighed 3.7 g and had a 16 cm external whip antenna. Maximum battery life of transmitters was estimated by the manufacturer at ~150 days. We tracked radio-marked White-winged Doves using a vehicle-mounted, omni-directional antenna and hand-held H-antennas. Location points were recorded using a GPS unit (±4 m, *e*trex Vista, Garmin Corp., Shijr, Taiwan). We attempted to track each bird to a location point at least once every 7 days. We randomly placed radio-marked White-winged Doves into five groups of eight individuals (one group had 7 birds in 2002), with one group being tracked each day. The first group tracked was placed at the end of the rotation on consecutive weeks. Daily start times began an hour later each day during each week so that search periods for that group included the entire day (Small et al. 2005a).

We assumed White-winged Doves were feeding primarily within Waco and defined nesting home range as the area within Waco in which points of location were obtained for each nesting White-winged Dove. This included points associated with all activities during the nesting period. We calculated 95% and 50% Jennrich-Turner ellipses for each radio marked White-winged Dove with ≥10 location points (Biotas 1.2b, Ecological Software Solutions, Urnasch, Switzerland). We chose the Jennrich-Turner method because it was reasonable to assume nests would be near the center of the ellipse and movements around the nest to be random. Home range size estimates using this method are not a function of sample size (Jennrich and Turner 1969).

We designated 95% ellipses as nesting home range (the area in which an individual will be found with a confidence of 95%) and 50% ellipses as nesting core areas (the area in which a bird is likely to be present at least 50% of the time). We used two-sample *t*-tests to compare nesting home range size and nesting core area size between years for all individuals with ≥10 points and between genders for both years combined. We conducted two-sample *t*-test after $\log_e$ transforming data because it did not meet assumptions of normality and homoscedasticity. We conducted a power analysis because of small sample size and high variance. We did not use a two-way ANOVA because transmitters were implanted at different times of the year which did not represent true temporal replication. We also used a two-sample *t*-test on $\log_e$-transformed data to examine if nesting home range overlap differed between years for female doves. Males were not analyzed because there was no overlap of male nesting home range in 2003.

We used contingency tables to evaluate whether locating radio-marked White-winged Doves at nest or non-nest location points was dependent on year or gender. We used a two-sample *t*-test to compare non-migratory linear distance moved from trap site for recovered doves between years and ANOVA between gender and age group for doves banded in 2002. Movements were considered non-migratory if the dove was banded as a resident, movement occurred during the breeding season, or the movement was not in a southerly direction. All statistical analyses were conducted using S-Plus 7.0 (Insightful Corp, Seattle, WA, USA) and SYSTAT (Systat Software, Inc., Richmond, CA, USA) software with $\alpha = 0.05$ (Sokal and Rohlf 1995).

RESULTS

Nesting home range and nesting core areas for individuals with ≥10 location points by gender and year varied. Mean (± SE) nesting home ranges of individuals with ≥10 location points for both years combined differed slightly by gender (females: $n = 17$, $\bar{x} = 75.7 \pm 30.0$ km^2; males: $n = 11$, $\bar{x} = 31.9 \pm 18.1$ km^2; $t_{26} = 1.1$, $P = 0.29$). The log$_e$-transformed data also did not differ ($t_{26} = 1.4$, $P = 0.17$). Power was low ($\beta = 0.24$, $\Delta = -43.72124$, $\alpha = 0.05$). Mean (± SE) nesting core areas for both years combined were 6.4 ± 3.6 km^2 for males and 17.5 ± 6.9 km^2 for females. Mean nesting home ranges for all individuals of known gender differed by year (2002: $n = 17$, $\bar{x} = 75.6 \pm 28.4$ km^2; 2003: $n = 11$, $\bar{x} = 32.0 \pm 23.7$ km^2; $t_{26} = 2.8$, $P < 0.001$). Mean (± SE) nesting core areas for all individuals of known gender were 17.5 ± 6.6 km^2 for 2002 and 6.4 ± 4.7 km^2 for 2003. Within year mean nesting home ranges for individuals differed by gender for 2002 (males: $n = 10$, $\bar{x} = 42.6 \pm 27.7$ km^2; females: $n = 7$, $\bar{x} = 98.7 \pm 43.9$ km^2; $t_{15} = 2.3$, $P < 0.001$) but did not differ for 2003 (males: $n = 7$, $\bar{x} = 13.2 \pm 11.0$ km^2; females: $n = 4$, $\bar{x} = 42.8 \pm 37.2$ km^2; $t_9 = 0.4$, $P = 0.69$).

Seventeen individuals of known gender in 2002 had ≥10 location points. Nesting home ranges overlapped for 8 of 10 females and five of seven males. Eleven individuals of known gender in 2003 had ≥10 location points. Nesting home ranges overlapped for three of seven females and zero of four males. The proportion of females and males with nesting home range overlap did not differ by year ($\chi^2_1 = 0.12$, $P = 0.73$ and $\chi^2_1 = 0.87$, $P = 0.35$, respectively) or by gender within years ($\chi^2_1 = 0.05$, $P = 0.82$ for 2002 and $\chi^2_1 = 0.27$, $P = 0.61$ for 2003).

The probability of locating radio marked white-winged doves with ≥10 location points to a nest versus a non-nest location site was dependent on year ($\chi^2_1 = 4.23$, $P = 0.04$) but not on gender, either between or within years (both years: $\chi^2_1 = 0.67$, $P = 0.41$; 2002: $\chi^2_1 = 0.95$, $P = 0.33$; 2003: $\chi^2_1 = 0.29$, $P = 0.59$).

Thirty-five (2.3%) of 1,517 birds banded in 2002 and 2003 were reported recovered (dead) as of March 2004. Mean distance (± SE) moved was 68.2 ± 17.6 km ($n = 35$). Distance moved did not differ by year ($n = 35$ [2002 = 25, 2003 = 10], $t_{33} = -0.3$, $P = 0.733$), gender for adults in 2002 only ($n = 18$ [7 male, 11 female], $t_{16} = 0.1$, $P = 0.908$), or by gender or age in 2002 only ($n = 24$ [7 male, 11 female, 6 HY], $F_{2,21} = 0.06$, $P = 0.942$). Band recoveries were not dependent on gender based on data from 2002 ($\chi^2_1 = 1.84$, $P = 0.18$). Distances of recoveries from banding sites ranged from 0 to 477.4 km (Table 1).

TABLE 1. Recovery data for White-winged Doves banded in Waco, Texas in 2002 and 2003 by distance from banding location.

Recoveries (*n*)	Distance (km)
18	0–20
7	20–50
2	50–100
4	100–200
3	200–300
0	300–400
1	>400

DISCUSSION

Nesting home range size did not differ between males and females between years and within 2003. However, nesting home range size of females was, on average, more than double that of males. This result was not entirely surprising because there is a distinct gender daily nest attendance pattern (Cottam and Trefethen 1968). Males typically attend the nest during the day with only mid-morning and late afternoon replacement. Females attend the nest at night with males generally roosting nearby. Consequently, more time is available for females to forage for food and water during which greater distances are likely to be traversed. Nest attentiveness may have limited core area movement explaining why core nesting range area and size did not differ by year or gender. Detecting a difference in nesting home range size by gender at $\alpha \leq 0.05$ and power of 0.70 would have required a sample size of ~45 radio-marked birds.

Gray (2002), in a similar study in Kingsville, Texas found no significant difference in home range size by gender for White-winged Doves ($t_{38} = 1.18$, $P = 0.246$) with males having a greater home range size ($\bar{x} = 29.66$ and 13.82 ha for males and females, respectively). However, home ranges were estimated using convex polygons and required a minimum of only five location points.

Male and female White-winged Doves were tracked to non-nest location points and nest location points with similar probability. Thus, future nesting studies of this species using radio telemetry need not preferentially select a particular gender. The probability of locating a radio-marked White-winged Dove to a nest was significantly higher in 2003 than in 2002. This seems reasonable because doves were monitored in early spring in 2003 versus midsummer in 2002.

The wide range of distances of band recoveries in this study and the lack of differences between year, gender, and age groups indicate that non-migratory movements may be an important component of gene flow and population establishment.

We located <50% of radio-marked White-winged Doves 60 days after implantation. A similar study in Kingsville, Texas (Small et al. 2005b) with a much smaller human population using identical transmitters had 81% of radio-marked doves located more than 60 days post-implant. Thus, differing levels of human development may affect reception quality of radio-transmitters.

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Population Estimates for Eurasian Collared-dove in Northeastern Colorado

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ABSTRACT.—Eurasian Collared-doves (*Streptopelia decaocto*) have colonized small rural towns throughout Colorado. We document their occurrence in 23 towns in Weld and Larimer counties in northeastern Colorado during the 2004 breeding season. Estimated population sizes in these towns ranged from 0 to 154 birds. Population increases were detected in 17 towns across the 2-month breeding season (Jun–Aug) with these increases ranging from 1.1- to 6.9-fold. We interpret these data as indicating successful breeding and expanding populations. These are the first reliable data on population sizes of Eurasian Collared-dove in North America and may benefit management strategies for this invasive species in Colorado and elsewhere in the Great Plains. *Received 23 June 2005. Accepted 1 September 2006.*

The Eurasian Collared-dove (*Streptopelia decaocto*) is capable of large range expansions due to several factors, including its vagility and high fecundity due to multiple broods (Robertson 1990). These doves tend to thrive around areas of human habitation, including suburbs, small towns, and agricultural settlements where they receive indirect supplementation of food from humans, such as grain (Smith 1987). The species was first reported on the western side of the Atlantic in the Bahamas in the 1970s. A small population was released when a local pet store in Nassau was burglarized, and the species spread to Florida by the early 1980s (Smith 1987). Its expansion in Florida was enhanced because of the long breeding season and the availability of human-supplemented food (Romagosa and Labisky 2000). Christmas Bird Counts in Florida suggested a 20-fold increase in population from 1986 to 1996 (Romagosa and Labisky 2000). Since expansion into Florida, the Eurasian Collared-dove has dispersed throughout the south, southwestern, and central United States and continues to spread north and west (Romagosa and McEneaney 2000). In Colorado (west-central USA), the Eurasian Collared-dove was first observed in 1996 (Truan and Percival 1996). Expansion of these doves throughout the state has occurred at a rapid pace since then with most counties now reporting the species (Colorado Field Or-

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nithologists 2006). This invasive species could have economic and ecological impacts, and its range expansion should be monitored. However, no reliable data exist on population sizes nor are there suggestions for how best to monitor these doves. This information could be used for the development of a management strategy for this invasive species in Colorado and elsewhere in the Great Plains.

Our objective was to quantitatively describe population sizes of Eurasian Collared-doves in small rural towns, and changes in population sizes during the 2004 breeding season (i.e., Jun–Aug). We also investigated how Farnsworth et al.'s (2002) survey methodology, with Alldredge et al.'s (2007) modifications, would perform with this species.

METHODS

We used a generalized auditory removal model (Farnsworth et al. 2002, Alldredge et al. 2007) to estimate population numbers of urban-dwelling birds in 23 small towns (population range 200–15,000) in Weld and Larimer counties in northern Colorado during 15–30 June and 11–31 August 2004. All towns were characterized as low-density residential developments within an agricultural region of the High Plains (elevation 1,400–1,615 m). We were confined to surveying birds along roads. We overlaid a grid of 25-m radius circles along all roads in each town and randomly selected 20 circles to survey in each town, except for Lucerne in which we surveyed all nine circles. A single observer (SMB) conducted a 4-min survey for each circle and noted whether each bird in the circle was detectable in each of four consecutive 1-min periods. We used these data to derive population density estimates using the full set of closed capture models incorporating time (t), behavior (b), and heterogeneity (h; following Pledger [2000] with a single mixture parameter) in Program MARK (White and Burnham 1999). We modeled these three classes of detection effects (t, b, h) individually and in concert. This led to seven general models (M_t, M_b, M_h, M_{tb}, M_{th}, M_{bh}, M_{tbh}) plus a model that ignores these effects (M_0) as well as the Farnsworth et al. (2002) model in which we set the behavior effect equal to zero. We modeled the effects as additive whenever there was more than one effect in a model. We modeled the detection process for all towns together (Conn et al. 2004, White 2005).

We explored possible violations of closure with CloseTest (Stanley and Burnham 1998, Stanley and Richards 2005) as well as the Pradel model (Pradel 1996, Boulanger et al. 2002).

Birds flying over or through a circle during a survey period were not included in the analysis. We used Akaike's Information Criterion with a small sample size correction (AIC_c) for model selection and present model-averaged estimates when more than one model had some explanatory ability (Burnham and Anderson 2002). Densities of doves were extrapolated to estimate the number of doves in June and in August based on the total sampling frame area that included all possible survey points.

RESULTS

The Eurasian Collared-dove was observed in all 23 towns within the study period. Seventy-nine doves were counted in June and 157 in August. A model incorporating temporal, behavioral, and heterogeneity effects (M_{tbh}) in detection probabilities best explained the June data with other models (M_b, M_{bh}) incorporating behavior and heterogeneity having some explanatory ability ($\Delta AIC_c < 6$). A model incorporating heterogeneity (M_h) was most supported for the August data, although models (M_{tbh}, M_{bh}, M_{th}) incorporating temporal and behavior effects also had some explanatory ability ($\Delta AIC_c < 3$). Many models had some explanatory ability and we performed model averaging to obtain population estimates (Table 1). We were unable to confirm closure using our closure test.

The mixture probability in the Pledger model for heterogeneity was 0.04 ($\widehat{SE} = 0.05$) and 0.09 ($\widehat{SE} = 0.04$) for June and August, respectively. The probabilities of detecting an individual bird, per 1-min period, ranged from 0.36 to 0.87 in June and from 0.28 to 0.91 in August. The probability of reobservation (the "behavior" effect) ranged from 0.19 to 0.79 in June and from 0.21 to 0.88 in August. The β value associated with the behavior effect was negative in June (-1.48 ± 0.58) and August (-0.38 ± 0.44).

Density estimates ranged from 0.00 to 2.58 individuals/ha for June and from 0.00 to 6.17

TABLE 1. Population estimates of Eurasian Collared-doves in June and August 2004 in each of 23 towns in northeastern Colorado.

Town[a] (sampling frame area [ha])	Month	Raw count	Density estimate /ha (CI)	Extrapolated population (CI)	Population change (X-fold)
Ault (11.4)	Jun	4	1.02 (1.01–1.02)	12 (12–12)	
	Aug	19	6.17 (4.17–8.18)	70 (47–93)	6.05
Berthoud (38.7)	Jun	2	0.51 (0.51–0.51)	20 (20–20)	
	Aug	2	0.54 (0.26–0.82)	21 (10–32)	1.06
Eaton (16.5)	Jun	2	0.51 (0.51–0.51)	8 (8–8)	
	Aug	11	3.52 (2.17–4.86)	58 (36–80)	6.90
Fort Lupton (31.8)	Jun	5	1.27 (1.27–1.28)	41 (40–41)	
	Aug	9	2.85 (1.68–4.02)	91 (53–128)	2.24
Frederick (29.8)	Jun	8	2.05 (1.90–2.21)	61 (57–66)	
	Aug	16	5.18 (3.41–6.94)	154 (102–207)	2.52
Galeton (5.5)	Jun	0	0.00 (0.00–0.00)	0 (0–0)	
	Aug	3	0.86 (0.35–1.38)	5 (2–8)	—[b]
Gilcrest (11.6)	Jun	4	1.02 (1.01–1.02)	12 (12–12)	
	Aug	17	5.51 (3.66–7.35)	64 (43–85)	5.40
Gill (4.9)	Jun	3	0.76 (0.76–0.76)	4 (4–4)	
	Aug	9	2.85 (1.68–4.02)	14 (8–20)	3.73
Hudson (12.0)	Jun	9	2.31 (2.14–2.49)	28 (26–30)	
	Aug	8	2.52 (1.44–3.60)	30 (17–43)	1.09
Johnstown (13.2)	Jun	2	0.51 (0.51–0.51)	7 (7–7)	
	Aug	3	0.86 (0.35–1.38)	11 (5–18)	1.69
Keenesburg (11.6)	Jun	3	0.76 (0.76–0.76)	9 (9–9)	
	Aug	2	0.54 (0.26–0.82)	6 (3–10)	0.71
Kersey (12.8)	Jun	1	0.25 (0.25–0.25)	3 (3–3)	
	Aug	1	0.25 (0.25–0.26)	3 (3–3)	1.00
LaSalle (17.3)	Jun	7	1.79 (1.67–1.91)	31 (29–33)	
	Aug	12	3.85 (2.42–5.28)	67 (42–91)	2.15
Lochbuie (16.1)	Jun	2	0.51 (0.51–0.51)	8 (8–8)	
	Aug	3	0.86 (0.35–1.38)	14 (6–22)	1.69
Lucerne (1.8)	Jun	2	1.13 (1.13–1.13)	2 (2–2)	
	Aug	0	0.00 (0.00–0.00)	0 (0–0)	—[b]
Mead (6.5)	Jun	10	2.58 (2.38–2.77)	17 (15–18)	
	Aug	8	2.52 (1.44–3.60)	16 (9–23)	0.98
Milliken (23.4)	Jun	1	0.25 (0.25–0.25)	6 (6–6)	
	Aug	0	0.00 (0.00–0.00)	0 (0–0)	—[b]
Nunn (8.6)	Jun	0	0.00 (0.00–0.00)	0 (0–0)	
	Aug	9	2.85 (1.68–4.02)	25 (14–35)	—[b]
Pierce (12.6)	Jun	8	2.05 (1.90–2.21)	26 (24–28)	
	Aug	14	4.51 (2.92–6.11)	57 (37–77)	2.20
Platteville (16.9)	Jun	4	1.02 (1.01–1.02)	17 (17–17)	
	Aug	5	1.52 (0.72–2.33)	26 (12–39)	1.49
Severance (5.3)	Jun	1	0.25 (0.25–0.25)	1 (1–1)	
	Aug	1	0.25 (0.25–0.26)	1 (1–1)	1.00
Wellington (26.5)	Jun	0	0.00 (0.00–0.00)	0 (0–0)	
	Aug	1	0.25 (0.25–0.26)	7 (7–7)	—[b]
Windsor (64.2)	Jun	1	0.25 (0.25–0.25)	16 (16–16)	
	Aug	4	1.18 (0.55–1.82)	76 (35–117)	4.65

[a] All towns in Weld County, except Berthoud and Wellington, which are in Larimer County.
[b] — = Could not be estimated due to denominator = 0.

individuals/ha for August in the 23 towns we studied (Table 1). Extrapolated abundance estimates ranged from 0 to 61 birds in June and from 0 to 154 birds in August. Extrapolated abundance estimates increased from June to August in 17 towns (74%), with nontrivial increases (i.e., 95% confidence intervals not overlapping) occurring in 12 towns. Populations increased from 2.2- to 6.9-fold in these 12 towns.

DISCUSSION

The Eurasian Collared-dove is an exotic species in North America that is dispersing rapidly and now resides throughout much of Colorado. The habitat (i.e., rural farming communities) in northeastern Colorado is similar to Collared-dove breeding habitat in Eurasia (Smith 1987). We documented a substantial and widespread population of Eurasian Collared-doves in small northeastern Colorado towns. We also documented increasing populations from June to August, most likely indicating successful breeding and dispersal. Nest success, fecundity, and survival of offspring were not measured directly and our models relied upon several unconfirmed assumptions—the most important being geographic closure (i.e., no movement in or out during the 4-min survey period). We did not detect closure in our modeling, but the behavior effect we observed could have confounded our closure test. In essence, an individual leaving during the sampling period cannot be distinguished from an individual that becomes less detectable (either due to the bird's or observer's behavior). Other assumptions were that no births or deaths occurred during each 4-min observation period, birds were identified correctly, and double counting did not occur.

The negative behavior effect detected was unexpected. This negative effect may be explained in that most detections were of an auditory nature and that resident birds may have been less likely to vocalize after calling once.

We suggest giving attention to the survey location selection process when surveying species such as the Eurasian Collared-dove. We could not survey off roads due to logistics. Thus, we randomly chose locations along roads from which to survey in the small towns and only extrapolated to these areas. Much of each town could be observed from roads, but being able to survey off-road locations would be an improvement in future studies.

The actual population size of Eurasian Collared-doves in Colorado, or in any state in the United States, remains unknown. Our data suggest the population size of this dove may be substantial. Thus, concern over how such an invasive population of an exotic species may influence native avifauna through competition or disease may be warranted. One possible effect of increased populations of the Eurasian Collared-dove is that it may outcompete native avifauna for resources (Romagosa and Labisky 2000). The Eurasian Collared-dove has shown behavioral dominance over several species in Florida, including Mourning Dove (*Zenaida macroura*), White-winged Dove (*Z. asiatica*), Northern Cardinal (*Cardinalis cardinalis*), and Painted Bunting (*Passerina ciris*) (Romagosa and Labisky 2000).

Another possible effect is the risk of disease to indigenous species that the Eurasian Collared-dove may present. *Trichomonas gallinae* has been identified in the Eurasian Collared-dove in Europe (Romagosa and Labisky 2000). The Eurasian Collared-dove has also been shown to be an excellent reservoir for Newcastle disease, which can cause high mortality rates in chickens (Terregino et al. 2003) and wild birds such as cormorants (*Phalocrocorax* sp.) (Glaser et al. 1999). This exotic dove has yet to be associated with any disease epizootics in the United States, although it has been infected with mosquito-borne viruses such as St. Louis encephalitis virus and West Nile virus (NK, unpubl. data). Further studies to understand the demography of this dove and its influences on other avian species are needed.

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Diet of the Rufous-legged Owl (*Strix rufipes*) at the Northern Limit of its Distribution in Chile

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ABSTRACT.—We quantified the diet of the Rufous-legged Owl (*Strix rufipes*) by analysing 63 pellets collected during 2003 and 2005 in a small coastal sclerophyllous forest stand at the northern limit of its distribution in Chile (31–32° S). The diet comprised small mammals (frequency = 57.8%, biomass = 99.3%), crustaceans (frequency = 1.7%, biomass = 0.1%), and insects (frequency = 40.5%, biomass = 0.6%). We identified at least 10 small mammal species in these pellets of which Bennett's chinchilla rat (*Abrocoma bennetti*; frequency = 12.4%) and long-tailed pygmy rice rat (*Oligoryzomys longicaudatus*; frequency = 7.4%) were the most frequently occurring mammalian prey remains. Terrestrial small mammals accounted for 21.5% by frequency of all individuals and 49.1% of the total biomass; scansorial/arboreal small mammals accounted for only 13.2% of all individual prey and 17.2% of total biomass. *Received 14 February 2006. Accepted 18 July 2006.*

Forest fragmentation and land-use patterns have modified and dramatically reduced the availability and quality of natural habitats in Chile (Fuentes 1994). The distribution of both southern temperate and sclerophyllous forests has been significantly reduced. Sclerophyllous forest has virtually disappeared throughout its original distribution as a result of intensive human exploitation and destruction during the last 200 years. This forest type is now restrict-

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ed to small degraded patches along deep ravines in mountainous areas (Fuentes 1994, Estades and Temple 1999). There is an urgent need to understand the ecology of forest-specialist predators because native forests are critically threatened (Fuentes 1994).

The Rufous-legged Owl (*Strix rufipes*) is a critically threatened forest-specialist (Jaksic and Jiménez 1986, Martínez and Jaksic 1996, Jaksic et al. 2001, Omland et al. 2001) and is protected by law (República de Chile 1996, 1998). This owl is distributed from 33° to 56° S and inhabits the sclerophyllous forest of central Chile and the southern temperate forest in both southern Chile and Argentina (Díaz 1999, Couve and Vidal 2003). The diet of the Rufous-legged Owl has been relatively well documented in the southern temperate rainforest (Martínez 1993, Martínez and Jaksic 1997, Udrizar et al. 2005, Figueroa et al. 2006), but there is only one study in a sclerophyllous forest (Díaz 1999). Here, we report the Rufous-legged Owl's diet in a coastal sclerophyllous forest remnant at the northern limit of its range in Chile.

STUDY AREA

We studied the Rufous-legged Owl's diet in the Oasis la Campana Private Reserve (2,500 ha), Valparaíso region, central Chile. This Reserve is adjacent to La Campana National Park (31° 55′ S, 71° 08′ W) in the coastal mountain range. It is characterized by relatively rough topography (300–1,800 m elevation, slopes to 30–40°). The vegetation of the area is typical of the sclerophyllous forest sub-region (Gajardo 1994). The climate is Mediterranean-arid (di Castri and Hajek 1976) with mean annual rainfall and temperature being 100–118 mm and 20° C, respectively (Saiz et al. 1989, Pliscoff 2002).

METHODS

We collected 63 pellets under roost trees during January (austral summer; $n = 7$), August-September (winter; $n = 20$), November (spring; $n = 8$) 2003, July 2005 (winter; $n = 13$), and December 2005 (spring; $n = 15$) in a forest stand covering a small ravine. Pellets represented at least one resident Rufous-legged Owl pair. The forest stand was composed of sclerophyllous (*Cryptocarya alba* [dominant], *Peumus boldus*, *Schinus latifolius*) and higrophyllous (*Aristotelia chilensis*, *Beilschmiedia miersii*, *Dasyphyllum excelsum*, *Drymis winteri*) trees. There were also interspersed palm trees (*Jubaea chilensis*) in this forest stand. Tree height and dbh (diameter at breast height) ranged from 10 to 25 m and 10 to 100 cm, respectively. Canopy cover ranged from 50 to 80%, and the understory was sparse and mostly composed of *Escallonia* spp., *Maytenus boaria*, *Equisetum bogotense*, and saplings of native trees.

We identified and quantified small mammals in the pellets on the basis of skulls or tooth pairs (whichever gave the highest count) following Reise (1973) and Pearson (1995). Insects were identified and quantified by head capsules or elytra following Peña (1986) and Saiz et al. (1989). Infrequent prey remains were identified using reference collections and were quantified by diagnostic body elements. We identified prey items to the lowest possible taxonomic category. We estimated biomass contribution of each prey type in the diet by multiplying the number of individuals in pellets by the mean body mass of that prey item (Marti 1987). Body mass of prey was obtained from the literature and authors' unpublished data. We assumed that unidentified prey biomass was similar to the mean mass of the most closely related identified taxa. We pooled results from all individual pellets for data analysis due to the small seasonal sample sizes.

RESULTS

Most pellets were broken or distorted during collections and only a few could be measured. Whole pellets averaged 38.5 ± 2.5 mm in length × 19.2 ± 1.0 mm in width ($\bar{x} \pm$ SE) and had a mean dry weight of 2.05 ± 0.22 g ($n = 9$). Ten small mammal species, one crab, and insects belonging to two orders were identified in the pellets. Small mammals and insects were the most consumed prey, but mammals constituted most of the biomass (Table 1). Bennett's chinchilla rat (*Abrocoma bennetti*), long-haired mouse (*Abrothrix longipilis*), long-tailed pygmy rice rat (*Oligoryzomys longicaudatus*), and introduced rats (*Rattus* spp.) were the most important small mammal prey (Table 1). All identified mammalian prey species were forest dwellers. Scansorial/arboreal small mammals accounted for 13.2% of

TABLE 1. Diet of the Rufous-legged Owl based on pellets (n = 63) during 2003 and 2005 in a coastal sclerophyllous forest remnant in the Oasis La Campana Private Reserve, central Chile. PF = percent frequency, PB = percent biomass.

Prey taxa	Mass (g)[a]	Habits[b]	PF	PB
Mammals			57.8	99.3
Abrocoma bennetti	219	T	12.4	38.2
Octodon bridgesi	180	T	0.8	2.1
O. lunatus	180	T	0.8	2.1
Phyllotis darwini	66	T	2.5	2.3
Abrothrix longipilis	76	T	3.3	3.5
A. olivaceus	40	T	1.7	0.9
Chelemys megalonix	62	T	0.8	0.7
Oligoryzomys longicaudatus	45	S	7.4	4.7
Rattus spp.	200	S	4.1	11.6
Thylamys elegans	40	A	1.7	0.9
Unidentified small mammals	108		22.3	32.3
Crustaceans			1.7	0.1
Aegla spp.	3		1.7	0.1
Insects			40.5	0.6
Orthoptera	1		1.7	*
Coleoptera	1		38.8	0.6
Total prey items	121			
Total prey biomass (g)	8,680			

[a] Body mass from Díaz (1999) except for *C. megalonix*, *Aegla* spp., and insects (unpubl. data).
[b] Habits from Martínez (1993), Díaz (1999), and authors' unpublished data: A = arboreal, S = scansorial, T = terrestrial.
* Percent biomass < 0.05 g.

all individual prey and 17.2% of total biomass; terrestrial small mammals accounted for 21.5% of all individuals and 49.1% of total biomass (Table 1). We identified at least five species of insects taken as prey: *Cratomellus armatus* (Orthoptera), *Ferionomorpha aerea*, *Strongylaspis limae*, *Aulacopalpus ciliatus*, and *Brachysternus* spp. (Coleoptera).

DISCUSSION

Our findings are similar to those reported by Díaz (1999) for Rufous-legged Owls in the Andean sclerophyllous forest of Río Clarillo National Reserve (50 km southeast from Oasis La Campana). Díaz (1999) found that mammalian prey accounted for most of the biomass (>97% of all prey) with Bennett's chinchilla rat being most important (19% of all biomass). Rufous-legged Owls in Oasis La Campana appeared to consume more long-tailed pygmy rice rats and *Rattus* spp. than in Río Clarillo; the inverse was true regarding the moon-toothed degu rat (*Octodon lunatus*). Scansorial/arboreal small mammals accounted for 17% of the biomass consumed by Rufous-legged Owls in Oasis La Campana, whereas they constituted only 8% of the biomass consumed in Río Clarillo. It is possible these differences are an artifact of our small sample size reflecting only one pair of owls.

Rufous-legged Owls in sclerophyllous forests appear to prey more on terrestrial than on arboreal/scansorial small mammals (Díaz 1999, this study) in contrast to results reported for southern Chilean temperate forests (Martínez 1993; Martínez and Jaksic 1996, 1997; Figueroa et al. 2006). Díaz (1999) attributed these differences to small forest remnants in central Chile that had open midstory (which could make terrestrial small mammals more prone to predation by owls) and low quality of forest patches causing owls to hunt in adjacent open areas. It is also possible that presence of gaps in the forest make cursorial/fossorial small mammals more detectable by Rufous-legged Owls (Udrizar et al. 2005). The dense midstory of southern temperate forest stands may restrict Rufous-legged Owls to search for prey inhabiting the overstory or forest canopy. Figueroa et al. (2006) suggested the distribution, abundance, and size of prey as well as prey behavior could also be involved.

It is possible that predation on scansorial small mammals by Rufous-legged Owls in sclerophyllous forests was underestimated because the climbing ability of Bennett's chinchilla rat is not well known. Mann (1978) and Díaz (1999) indicate this rodent is primarily a terrestrial species, but Díaz (1999) also indicates that it occasionally climbs trees. We frequently found activity signs of Bennett's chinchilla rat (e.g., feces, hairs) on branches of older trees (dbh > 0.5 m) 2–3 m above ground. Thus, it is possible that Bennett's chinchilla rats were captured on trees rather than on the ground. Our findings also indicated that Rufous-legged Owls were able to capture small mammals within a variable range of weights (40–219 g). We do not know if owls preyed opportunistically (on more abundant prey) or selected them according to body size. More studies are necessary to better understand the ecology of the Rufous-legged Owl in the sclerophyllous forest remnants of central Chile.

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Locality Related Changes in the Diet of the Barn Owl (*Tyto alba stertens*) in Agroecosystems in Central Punjab, Pakistan

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ABSTRACT.—We studied spatial differences in Barn Owl (*Tyto alba stertens*) diets in agroecosystems of six districts of central Punjab, Pakistan. Analysis of pellets collected over 3 years revealed the house shrew (*Suncus murinus*) dominated all diets. This species constituted 75.0% of the diet in the Sheikhupura District, 68.4% in the Okara District, 67.2% in the Faisalabad District, 65.6% in the Toba Tek Singh District, 59.3% in the Jhang District, and 56.3% in the Hafizabad District. Rats and mice together formed 28% of the overall diet while birds (4.2%) were consumed more than bats (2.0%). The greatest diversity in Barn Owl diets was in the Jhang District. *Received 21 July 2006. Accepted 19 November 2006.*

The Barn Owl (*Tyto alba*) is universally acknowledged for its use of rodents and other small mammals as food. Thus, this species is thought to have an important role in control of potential agricultural pests (Duckett 1991, Mohammad and Goh 1991, Lee 1997, Lekunze et al. 2001). The diet of the Barn Owl in most parts of the world is well documented but information on this species in Asia and particularly southern Asia is generally poor. Mason and Lefroy (1912), Ali and Ripley (1969), and Roberts (1991) have been the main sources of information on Barn Owls in southern Asia, More recently, Mahmood-ul-Hassan et al. (2000) presented information on the food habits of the Barn Owl in central Punjab, Pakistan.

Our objectives were to: (1) investigate the food habits of the Barn Owl in the six districts of central Punjab, and (2) compare locality-related diversity in diets.

METHODS

We collected 1,163 pellets of Barn Owls from 11 sites in Faisalabad District (31° 25′ N, 73° 07′ E), 394 from 4 sites in Jhang District (31° 16′ N, 72° 19′ E), 342 from 4 sites in Hafizabad District (32° 04′ N, 73° 41′ E) and 388 from 2 sites in Sheikhupura District (31° 42′ N, 73° 30′ E). We also had small samples of Barn Owl pellets collected from single sites in Toba Tek Singh ($n = 37$) (30° 57′ N, 72° 28′ E) and Okara ($n = 36$) (30° 48′ N, 73° 27′ E) districts. These sites were visited once every month during 3 years. Pellets were initially placed in polythene bags along with tags indicating date and locality of collection. Pellets were stored over night at 55° C before then being stored in paper bags. Each pellet was then analyzed to identify remnants of Barn Owl prey. We counted mammalian skulls to ascertain the number of prey items present in each pellet. If skulls were absent, pairs of mandibles or numbers of atlas vertebrae were counted. We identified mammalian prey to

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species level from skulls and teeth using reference skulls of small mammals known to be present in the study area (Mahmood-ul-Hassan et al. 2000).

The data obtained were used to assess the locality-related diversity of the prey fauna represented in the Barn Owl pellets. We used three indices: (1) species richness (S), (2) Shannon's index (H′), and (3) Peilou's evenness (E) to assess and compare the diversity (Magurran 1988) in the diet of Barn Owls.

RESULTS

Diet Composition.—Shrews and rodents were the main staples of the diet of Barn Owls in the six districts of Punjab (Table 1). Shrews (65.6%) were taken more frequently than rodents (27.8%). The soft-furred field rat (*Rattus meltada*) and the bandicoot rat (*Bandicota bengalensis*) were the rodents most often taken. Soft-furred field rats were consumed most by owls in the Toba Tek Singh District and least by owls in the Okara District whereas bandicoot rats were consumed most often in the Okara (10.5%) and Haifizabad (9.4%) districts, and least in the Sheikhupura (5.4%) District. The proportions of these rats in the remaining districts ranged from 3.8 to 7.3% and 5.4 to 7.4%, respectively. The averages for these two species in the six districts were 6.2% and 6.5% (Table 1).

The house rat (*Rattus rattus*) was consumed more in Hafizabad (4.4%) and Faisalabad (4.2%) districts than in the other four districts; its proportion in the diet of Barn Owls in the six districts ranged from 1.6 to 4.4% with an average of 3.5%. The house mouse (*Mus musculus*) comprised from 1.3 to 4.3% (mean = 2.5%) in the diets of the owls in the six districts The proportion of the little Indian field mouse (*M. booduga*), which was not recorded in the Hafizabad sample, varied from 1.4 to 4.8%; the average for the six districts was 2.5%. The short-tailed mole rat (*Nesokia indica*) was represented in samples of pellets in all six districts; its proportions ranged from 1.2% (Hafizabad) to 3.5% (Okara) (mean = 1.6%) (Table 1).

The proportion of the Indian gerbil (*Tatera indica*) in pellets from the six districts varied from 0.6% (Sheikhupura) to 2.4% (Jhang) and averaged 1.6%. The contribution of the bush rat (*Gollunda ellioti*) to the diet of the Barn Owl was relatively small. It was represented only in the samples from Faisalabad, Jhang, and Hafizabad with an average proportion of 0.3% (Table 1).

Diversity.—The greatest diversity in the diets of Barn Owls was in Jhang District (Table 2) and differed among Sheikhupura (t = 4.47, df = 4, $P < 0.05$), Toba Tek Singh (t = 5.02, df = 6, $P < 0.01$), and Okara (t = 7.51, df = 10, $P < 0.01$) districts. The diet at Faisalabad was more diverse than in Sheikhupura (t = 3.11, df = 4, $P < 0.05$) and Toba Tek Singh districts (t = 4.51, df = 2, $P < 0.05$) (Table 3).

DISCUSSION

Shrews are the preferred prey of the Barn Owl throughout the world (Glue 1974, Lovari et al. 1976, deBruijn 1979, Bose and Guidali 2001, McGhie 2001). Their noisy conflicts and territorial behavior make them vulnerable to predation (Cody 1982, Churchfield 1990). Furthermore, once located they are easier to catch than rats and mice (Fast and Ambrose 1976, Nishimora and Abe 1988, Derting and Cranford 1989). The Barn Owl population in central Punjab, Pakistan exhibited a strong preference for house shrews (*Suncus murinus*). It was the staple food item and was predominant in the diets of Barn Owls inhabiting the agroecosystems of central Punjab, Pakistan.

Wheat-sugarcane, wheat-rice, and wheat-rice-sugarcane are the predominant agroecosystems of central Punjab. Wheat is sown mainly from late October through early December and is harvested from mid-April through early May. Transplantation of rice occurs during June and July and harvesting extends from late September through early November. The cane crop is the most stable habitat for rodents in croplands as it remains much longer than any other crop grown in the area. Cane harvesting starts in October and continues until late spring after which small scattered patches are left in the fields to be used as seed. These stands of cane provide shelter for rats and mice longer than any other crop in the study area. The cover provided by this crop greatly affects prey capture efficiency of Barn Owls (Munoz and Muroa 1990, Duckett 1991) and the owl is not able to exploit the murids in proportion to their abun-

TABLE 1. Relative frequency (%) of prey items in Barn Owl pellet samples from six sites in central Punjab, Pakistan (M = number of pellets, *n* = number of prey items in M, * unidentified rats).

	Locality (1–6) and % Relative abundance (*n*)						
	1	2	3	4	5	6	Combined
Prey items	M = 342	M = 388	M = 1,163	M = 394	M = 37	M = 36	M = 2,360
Shrews	56.3 (271)	75.0 (403)	67.2 (1,085)	59.3 (348)	65.6 (40)	68.4 (39)	65.6 (2,186)
S. murinus	56.1 (270)	75.0 (403)	67.2 (1,085)	59.2 (346)	65.6 (40)	68.4 (39)	65.5 (2,183)
S. etruscus	0.2 (1)			0.3 (2)			0.1 (3)
Squirrel		0.2 (1)	0.1 (2)	0.5 (3)			0.2 (6)
F. pennanti		0.2 (1)	0.1 (2)	0.5 (3)			0.2 (6)
Rats & mice	36.7 (176)	22.0 (118)	27.5 (444)	26.3 (153)	32.8 (20)	28.1 (16)	27.8 (927)
R. rattus	4.4 (21)	1.9 (10)	4.2 (68)	2.6 (15)	1.6 (1)	1.8 (1)	3.5 (116)
R. meltada	5.6 (27)	5.4 (29)	7.3 (117)	3.8 (22)	16.4 (10)	1.8 (1)	6.2 (206)
M. musculus	4.4 (21)	1.3 (7)	2.5 (40)	2.2 (13)	1.6 (1)	5.3 (3)	2.5 (85)
M. booduga	4.8 (23)	4.3 (23)	1.6 (26)	1.4 (8)		3.5 (2)	2.5 (82)
B. bengalensis	9.4 (45)	5.4 (29)	5.6 (90)	7.4 (43)	6.6 (4)	10.5 (6)	6.5 (217)
N. indica	1.2 (6)	1.5 (8)	1.7 (28)	1.4 (8)	3.3 (2)	3.5 (2)	1.6 (54)
T. indica	2.1 (10)	0.6 (3)	1.4 (23)	2.4 (14)	1.6 (1)	1.8 (1)	1.6 (52)
G. ellioti	0.2 (1)		0.1 (1)	1.4 (8)			0.3 (10)
UR*	4.6 (22)	1.7 (9)	3.2 (51)	3.8 (22)	1.6 (1)		3.1 (105)
Bats	1.9 (9)	1.1 (6)	1.8 (29)	3.8 (22)		1.8 (1)	2.0 (67)
Birds	4.8 (23)	1.7 (9)	3.0 (49)	9.9 (58)		1.8 (1)	4.2 (140)
Herptiles	0.3 (2)		0.2 (4)				0.1 (6)
Insects			0.1 (1)		1.6 (1)		0.1 (2)
Totals	481	537	1,614	584	61	57	3,334

1. Hafizabad District.
2. Sheikhupura District.
3. Faisalabad District.
4. Jhang District.
5. Toba Tek Singh District.
6. Okara District.

TABLE 2. Prey diversity in the diet of the Barn Owl in central Punjab, Pakistan.

	Richness (S)	Diversity (H')	Evenness (E)
Hafizabad	14	1.38	0.52
Sheikhupura	12	1.09	0.44
Faisalabad	15	1.36	0.50
Jhang	14	1.59	0.60
Toba Tek Singh	9	1.20	0.55
Okara	10	1.01	0.44

dance in cane dominated agroecosystems of central Punjab. However, after harvesting in wheat-rice based systems, rodents disperse in search of shelter (Beg and Rana 1978; Beg et al. 1981, 1983, 1986; Khan and Beg 1990; Mushtaq-ul-Hassan et al. 1998, 1999) making them vulnerable to Barn Owl predation.

Central Punjab is densely populated by humans. Villages, farm houses, and small clusters of adobe houses are present throughout the study area. The house shrew is at home in and around human settlements in croplands. House mice are also common in human settlements as well as farmlands (Ubaidullah et al. 1989, Khan and Beg 1990, Naz et al. 1997, Mushtaq-ul-Hassan et al. 1998). This is not the case with the house rat which is largely an indoor species in Pakistan. Thus, there is a variety of habitats within the home range of Barn Owls.

Our analysis suggests the Barn Owl does not affect pest rats and mice of agriculture in central Punjab. The Barn Owl has apparently no adverse impact on rodent populations because of (1) multi-cropping, which results in the development of a mosaic system where a variety of crops provide protective cover to rodents for the larger part of the year; and (2) the house shrew is the most common prey. The abundance of Barn Owls in croplands could be enhanced by installing nest boxes throughout croplands and by providing perches at strategic points in the fields.

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TABLE 3. Diversity of Barn Owl prey in the six districts of central Punjab, Pakistan. * = $P < 0.05$, ** = $P < 0.01$.

Hafizabad	Sheikhupura	Faisalabad	Jhang	T. T. Singh[a]	Okara
	NS	NS	NS	NS	NS
	Sheikhupura	S*	S*	NS	NS
		Faisalabad	NS	S**	NS
			Jhang	S**	S**
				T. T. Singh[a]	NS
					Okara

[a] Toba Tek Singh.

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Diets of Urban Breeding Barn Owls (*Tyto alba*) in Tel Aviv, Israel

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ABSTRACT.—Examination of 193 whole pellets and a number of partial pellets of a pair of Barn Owls (*Tyto alba*) in Neve Shiret, a neighborhood of Tel Aviv, Israel during the 2005 and 2006 breeding seasons revealed a total of 711 prey specimens. Six species of small mammals comprised 99.3% of the diet with a frequency of occurrence of 100% in pellets. Levant voles (*Microtus socialis guentheri*) (48.1%) and house mice (*Mus musculus*) (32.9%) were the most common prey species. The Barn Owl pair hunted in croplands adjacent to an urban residential area. *Received 19 August 2006. Accepted 25 November 2006.*

The diet of Barn Owls (*Tyto alba*) is well known throughout the world because of their cosmopolitan distribution and ease of pellet analysis (Taylor 1994), a method that accurately represents what they consume (Raczynski and Ruprecht 1974). The diet of urban dwelling Barn Owls is poorly known in Israel as most studies have concentrated in semi-desert, desert (Pokines and Peterhans 1997, Yom-Tov and Wool 1997, Tores and Yom-Tov 2003), and agricultural (Kahila 1992, Tores et al. 2005) areas. Our objective was to investigate the diet of a Barn Owl pair breeding in a residential neighborhood of Tel Aviv, Israel.

METHODS

A Barn Owl pair was found breeding from 2003 to 2006 in a building in northeast Tel Aviv in the neighborhood of Neve Sharet (32° 05′ N, 34° 46′ E). The neighborhood consisted of approximately 150 buildings most of which were three to six story tall apartment buildings. The nest was in a hollow in the wooden roof built over the window of a three-story apartment. The building was 300 m from the nearest croplands and citrus orchards. The regurgitated pellets of the Barn Owls were collected from under the nest after the nestlings fledged in the 2005 and 2006 breeding seasons. The number of eggs or chicks could not be ascertained as the nest was not accessible. However, three young were observed fledging from this nest in early July during both the 2005 and 2006 breeding seasons.

All pellets were brought into the laboratory and soaked in water for 4 days; whole pellets were dissected individually while partial pellets were grouped together. Mandibles, skulls, and femurs of mammals and wings of beetles were separated and identified. Data are presented as the minimum number of individuals (MNI) and percent frequency of occurrence, which is the proportion of the total number of pellets containing a given prey item. Body mass of rodents was calculated by averaging mean male and female weights provided in Mendelssohn and Yom-Tov (1999).

RESULTS

Eighty-two and 111 whole pellets, and a number of partial pellets were collected during the 2005 and 2006 breeding seasons, respectively. These pellets contained at least 711 prey specimens (Table 1). There was a significant difference ($\chi^2 = 46.37$, $P < 0.001$). between the 2 years in frequency of prey species. However, we pooled both years because Barn Owls are opportunistic predators. The differences observed were most likely caused by prey abundance. The assemblage was comprised mainly of small mammals (99.3%), which occurred in 100% of the pellets. The Levant vole (*Microtus socialis guentheri*) was the most common prey (48.1%) by number and occurred in 61.1% of the pellets, followed by house mice (*Mus musculus*) (32.9%) and Tristram's jirds (*Meriones tristrami tristrami*) (9.7%) in 38.3% and 17.6% of the pellets, respectively. The lesser white-toothed shrew (*Crocidura suaveolens monacha*) (7.5%) and blind mole rat (*Spalex leucodon ehrenbergi*) (0.6%) occurred in only 9.8% and 1.6% of the pellets. The remains of four black rats (*Rattus rattus rattus*) were found in broken pellets. Remnants of four birds and one insect were also found. The average number of prey per pellet during 2005 (n = 80) and 2006 (n = 111) was 1.4 and 2.0 specimens.

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TABLE 1. The diet of Barn Owls breeding in Tel Aviv, Israel during the 2005 and 2006 breeding seasons (MNI = Minimum number of individuals, PF = percent frequency).

		2005		2006		All years	
	Species	MN	PF	MNI	PF	MNI	PF
Mammals							
	Crocidura suaveolens monacha	11	5.3	42	8.3	53	7.5
	Microtus socialis guentheri	114	55.1	228	45.2	342	48.1
	Meriones tristrami tristrami	24	11.6	45	8.9	69	9.7
	Rattus rattus rattus	3	1.4	1	0.2	4	0.6
	Mus musculus	54	26.1	180	35.7	234	32.9
	Spalex leucodon ehrenbergi	0	0.0	4	0.8	4	0.6
Aves							
	Passer domesticus	0	0.0	2	0.4	2	0.3
	Columbidae	0	0.0	2	0.4	2	0.3
Arthropods							
	Coleoptera	1	0.5	0	0.0	1	0.1
Total individuals		207		504		711	

DISCUSSION

All prey species are known to occur within the area (Mendelssohn and Yom-Tov 1999). The pair of Barn Owls appeared to forage more frequently in croplands adjacent to Neve Sharet since Levant vole and Tristram's jirds do not inhabit urban areas. However, house mice and black rats occur in both habitats.

Common Kestrels (*Falco tinnunculus*) in urban areas of Israel (M. Charter, unpubl. data) and Europe (Yalden 1980, Pikula et al. 1984, Kübler et al. 2005) switch their diet from small mammals to birds due to the low availability of small mammals in cities. Unlike the Common Kestrel, the Barn Owl in Israel is a small mammal specialist (Pokines and Peterhans 1997, Yom-Tov and Wool 1997, Tores and Yom-Tov 2003, Tores et al. 2005).

The Barn Owls in this study were able to breed in the city by hunting in agricultural areas as mammals living in agriculture formed the majority of their diet. Nest site and prey availability are two of the major factors affecting distribution of raptor populations (Newton 1979) and it is unclear which is most lacking.

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Nest Usurpation by Red-headed Woodpeckers in Southeastern Montana

William J. Kronland[1]

ABSTRACT.—Red-headed Woodpeckers (*Melanerpes erythrocephalus*) occasionally usurp nests of other species. I compared incidence of nest usurpation in logged and non-logged treatments in a burned ponderosa pine (*Pinus ponderosa*) forest in 2004 and 2005. I predicted that usurpation would occur more often on logged than non-logged sites because Red-headed Woodpeckers tend to nest in more open habitats. Red-headed Woodpeckers nested more often and usurped a greater proportion of host species in logged ($n = 6$) than non-logged ($n = 3$) areas, despite host cavities being more abundant on the non-logged treatment. Usurping Red-headed Woodpecker pairs initiated nesting earlier ($\bar{x} = 12$ May ± 2 days) than pairs that excavated cavities (18 May ± 2 days) which implies an existing benefit to offset the cost of interspecific conflict. *Received 14 November 2005. Accepted 19 November 2006.*

Competition for nest sites is often intense among cavity nesting birds because potential sites are limited by specific habitat requirements, such as tree decay and stand density (Short 1979, Dobkin et al. 1997, Schepps et al. 1999, Hutto and Gallo 2006). Once a territory is obtained, nest cavity construction requires a substantial energetic investment with excavation ranging from 3 weeks for Hairy Woodpeckers (*Picoides villosus*) to over a year for Red-cockaded Woodpeckers (*P. borealis*) (Kilham 1983, Ligon et al. 1986). The high energetic investment appears offset by the high rate of reproductive success that cavity nests provide (Nice 1957, Oniki 1979).

Woodpeckers may reduce the cost of excavation by usurping cavities occupied by other species. Red-headed Woodpeckers (*Melanerpes erythrocephalus*) typically reuse or excavate their own cavities, but may occasionally usurp nests and consume eggs or nestlings of other cavity nesting species (Beal 1911, Schwab and Monnie 1959, Smith et al. 2000). The extent to which Red-headed Woodpeckers usurp nests rather than excavate their own has not been investigated.

Interspecific competition among cavity nesting birds can increase as nest site availability decreases (Brawn 1990, Lindell 1996). Red-headed Woodpeckers tend to nest in more open habitats (Smith et al. 2000) and greater density of woodpeckers in logged areas may result in limited nest site availability.

I recorded incidence of nest usurpation by Red-headed Woodpeckers as part of a 2-year study on the ecology of cavity nesting birds in a burned ponderosa pine (*Pinus ponderosa*) forest in southeastern Montana. The area had been logged in 2003 following a stand-replacement wildfire the previous year. Red-headed Woodpeckers began arriving on the study site in early May after most other cavity nesters had already completed cavity excavation and nest building.

The objective of this study was to compare incidence of nest usurpation by Red-headed Woodpeckers in logged versus non-logged post-fire treatments. I predicted that usurpation by Red-headed Woodpeckers would be greater in the logged than non-logged treatment.

METHODS

The study area was in a ponderosa pine forest ~40 km southeast of Ekalaka, Montana in the Long Pines unit of the Custer National Forest (45° 38′ N, 104° 11′ W). The study site (1,320 ha) is part of a larger forested area (28,368 ha) intermixed with pine savanna, open native grassland (*Achnatherum* spp., *Bouteloua* spp., *Carex* spp., and *Psuedoroegneria* spp.), and drainages dominated by green ash (*Fraxinus pennsylvanica*) and quaking aspen (*Populus tremuloides*). The area consisted of hills and rocky buttes (elevation 1,000–1,200 m) surrounded by lower elevation sagebrush (*Artemisia* spp.) shrubland, native grassland, and cultivated hayfields. Logged areas were treated in summer 2003 by removing all

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snags >25 cm diameter breast height (DBH). Snags were defined as any tree with <50% live green crown cover (U.S. Department of Agriculture 2003). Aspen and green ash trees were not harvested, and a 15-m no-cut buffer was left on either side of drainages to maintain watershed quality (U.S. Department of Agriculture 2003). Non-logged areas were not treated because of inaccessibility or excessive slope.

I examined incidence of nest usurpation by Red-headed Woodpeckers on logged (437 ha) and non-logged (444 ha) treatments from mid-April through 1 July in 2004 and 2005 (2 and 3 years post-fire). I recorded the number and status (alive or dead) of trees in circular plots (radius = 11.3 m) in 2005 to compare trees and snags per ha between treatments. I centered plots at random points (control: $n = 15$, salvage: $n = 19$) generated with a Minnesota Department of Natural Resources (DNR) extension for ArcView 3.0 software. Three subplots were arranged 120° from each other and 30 m from a central subplot (Martin et al. 1997).

I searched for nest cavities from 22 April to 1 July by using a random numbers table to place two plots (45–52 ha) in each treatment in 2004 and 2005. Landscape and salvage characteristics dictated the availability and size of contiguous search plots on the study site, which were smaller than the standard protocol for monitoring cavity nesting birds (200–400 ha) and likely reduced sample sizes (Dudley and Saab 2003). Plots were intensively searched every 1–2 days and nests were located by observing adults and systematically searching for cavities (Martin and Geupel 1993). Potential host species included Northern Flicker (*Colaptes auratus*), Hairy Woodpecker, Eastern Bluebird (*Sialia sialis*), Mountain Bluebird (*S. currucoides*), and European Starling (*Sturnus vulgaris*). I recorded the location of active nests with a Garmin E-trex Global Positioning System (GPS) receiver and flagged a bearing tree no closer than 30 m. Each cavity was visited every 3 days for up to 30 min, or until nest status (active or inactive) could be ascertained by observing an adult or nestling inside the cavity. I estimated nest phenology from courtship displays and duration of adult visits to the nest (courtship and egg laying vs. incubation), and food deliveries or nestling vocalizations (nestling stage) (Martin and Geupel 1993).

I monitored active cavities from time of location to completion of the nesting effort by observing nestling and adult behavior from >30 m. A nest was considered successful if fledglings were observed <20 m from the cavity, or if the fledgling date was known and the cavity did not show signs of predation (enlarged cavity entrance or feathers at base of tree) (Dudley and Saab 2003). Nests failed if predation was observed, or if nest stage was known and inactivity occurred before the likely fledgling date. Nest failures were probably underestimated because signs of predation are frequently not evident. A nest was considered usurped if Red-headed Woodpeckers were observed breeding in a cavity last used by a host species before fledging could have occurred. I estimated nest initiation for cavities discovered after the laying period by backdating from a known nest stage transition (Ehrlich et al. 1988, Martin et al. 1997). I did not examine nest success of Red-headed Woodpeckers because nest failures or fledglings were not observed before the survey period ended.

I pooled data from 2004 and 2005 and classified each Red-headed Woodpecker nest cavity as either usurped or excavated. I compared incidence of nest usurpation versus cavity excavation between salvage and control treatments with Pearson's Chi-square test. Sample sizes were small and I used Fisher's exact test to examine statistical significance. I also used a *t*-test to compare date of initiation for each Red-headed Woodpecker nest effort between pairs that usurped and excavated cavities.

RESULTS

The logged treatment contained fewer live trees ($\bar{x}$ = 3.1 ± 1.3 [SE]) and snags ($\bar{x}$ = 44.7 ± 4.9) per ha than live trees (12.2 ± 3.8) and snags (90.8 ± 8.5) on the non-logged treatment. Average size (cm) of green trees did not differ between treatments (logged: $\bar{x}$ = 5.5 DBH ± 13, non-logged: 15.5 ± 18), but snags were smaller in logged ($\bar{x}$ = 16.7 ± 1.9) than non-logged (23.7 ± 3.7) areas. I located and observed 91 active nest cavities in 2004 and 2005. Red-headed Woodpeckers were the only species that nested more often in the logged than non-logged treatment (Table 1). Red-headed Woodpeckers accounted

TABLE 1. Number of observed nest cavities per species in salvage logged and non-logged treatments in a burned ponderosa pine forest, Custer National Forest, Montana, 2004 and 2005.

Species	Logged	Non-logged
Northern Flicker	6	6
Red-headed Woodpecker	20 (6)[a]	11 (3)[a]
Hairy Woodpecker	7	13
Eastern Bluebird	3	5
Mountain Bluebird	5	10
European Starling	2	3

[a] Red-headed Woodpecker nests acquired by usurpation.

for 65% (n = 11) of nest failures of other cavity nesters by depredating two and usurping nine nests. More nests were usurped in the logged (n = 6) versus unlogged (n = 3) treatment, but incidence of nest usurpation versus construction by Red-headed Woodpeckers was similar between treatments ($\chi^2 = 0.03$, df = 1, $P = 1.0$). Nest cavities of potential host species were more abundant in the non-logged (n = 37) than logged treatment (n = 23). Thus, Red-headed Woodpeckers usurped a greater proportion of cavities in the logged (26%) than the non-logged (8%) treatment. Mountain Bluebirds were usurped most often (n = 5), followed by Hairy Woodpeckers (n = 3) and Northern Flickers (n = 1). Red-headed Woodpeckers were unsuccessful in their attempt to usurp one Hairy Woodpecker and one Northern Flicker nest cavity.

I used backdating to estimate nest initiation for one cavity that was discovered after the egg-laying period in 2005. The cavity was originally excavated by Hairy Woodpeckers the year before and, according to field notes, was probably unoccupied before Red-headed Woodpeckers enlarged the entrance and began nesting. Red-headed Woodpecker pairs that usurped cavities initiated nesting earlier ($\bar{x}$ = 12 May ± 2 days, n = 9) than pairs that excavated cavities (18 May ± 2 days, n = 22; t = 2.04, df = 21, P = 0.054).

DISCUSSION

I predicted that incidence of usurpation would be greater in logged than non-logged areas because Red-headed Woodpeckers tend to nest in open habitats (Smith et al. 2000, Doherty and Grubb 2002). Incidence of nest usurpation versus construction was nearly identical between treatments, but Red-headed Woodpeckers nested more often and usurped a greater percentage of hosts in logged than non-logged areas, despite host cavities being more abundant in the control.

Red-headed Woodpecker pairs that usurped cavities initiated nesting earlier than pairs that excavated cavities. Early nesting correlates with larger clutch sizes in cavity nesting birds (Dijkstra et al. 1982, Nilsson 1991). The benefit derived from usurping a nest was possibly countered by the risk associated with interspecific conflict. For example, Northern Flickers and Hairy Woodpeckers aggressively defended their cavities from Red-headed Woodpeckers. However, Mountain Bluebirds were seldom seen defending cavities against Red-headed Woodpeckers and were usurped almost twice as often as Hairy Woodpeckers, despite nests of the two species having occurred at similar abundances on each treatment.

Interspecific competition can increase as nest site availability decreases among cavity nesters (Brawn 1990, Lindell 1996). It seems logical that the similarity in incidence of usurpation versus excavation on my study site could be explained by availability of nest sites between treatments. An examination of nest site selection and availability by Red-headed Woodpeckers was beyond the scope of this study, but may be influenced by abundance of burned aspen stands (Vierling and Lentile 2006) or large relatively isolated conifer snags (pers. obs.). Most Red-headed Woodpecker nests were in large ponderosa pine snags (excavated: n = 20, usurped: n = 6) rather than aspen stands which were rare across the study area and infrequently used (excavated: n = 2, usurped: n = 3). Better understanding of the importance of hardwoods and distribution of snags is needed before nest site availability can be used to explain incidence of usurpation by breeding Red-headed woodpeckers in burned ponderosa pine forests.

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Presence of Wood Thrushes at a Nest Does Not Deter Parasitism by Brown-headed Cowbirds

Lyle E. Friesen,[1,4] Colin Zantinge,[2] and Holly Britton[3]

ABSTRACT.—There is scant information on whether Wood Thrushes (*Hylocichla mustelina*) are present at nests when Brown-headed Cowbirds (*Molothrus ater*) come to lay their eggs. We used miniature digital video cameras to document 10 visitations by cowbirds to five Wood Thrush nests. Cowbirds visited Wood Thrush nests on six occasions when host females were absent and aggressively approached incubating females on four other visits. Parental nest defense did not appear to be an effective deterrent to a challenge by a cowbird. Wood Thrushes were more tolerant of cameras early in the nesting season than after mid-June when they were more likely to accept the presence of cameras if they were gradually moved closer to nests over a period of several days. *Received 11 September 2006. Accepted 30 November 2006.*

The Wood Thrush (*Hylocichla mustelina*) is one of the more resilient neotropical migrant songbirds with respect to forest fragmentation (Friesen et al. 1999, Fauth 2001). However, its accommodation to breeding in forest patches within fragmented landscapes frequently brings it into contact with Brown-headed Cowbirds (*Molothrus ater*) that favor open and semi-open country, especially where there are wood-field ecotones (Lowther 1993). Cowbirds readily parasitize Wood Thrush nests, sometimes to the extent that host population stability is jeopardized (Trine 1998).

Numerous studies of Wood Thrushes in North America have reported high incidences of cowbird parasitism (Trine 1998, Fauth 2000). However, few data are available as to the presence or absence of Wood Thrushes at the time of nest parasitism. This paucity of information is not surprising given the challenges of unobtrusively observing activities at nests in low-light conditions in the 10–25 min before sunrise when female cowbirds typically parasitize nests (Scott 1991). Friesen et al. (1999) speculated that Wood Thrush nests were parasitized when the host females were absent. Thus, Wood Thrushes, which do not share incubation duties between males and females (Roth et al. 1996), might be more susceptible to parasitism than species such as Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) that do share incubation duties between males and females (Wyatt and Francis 2002), and that seldom leave their nests untended. If Wood Thrushes are present at nest sites when cowbird visitations occur, can they prevent cowbirds from gaining access to the nests? Wood Thrushes are about the same size ~40–50 g (Roth et al. 1996) as female cowbirds ~47.1 g (Lowther 1993). The larger size of Wood Thrushes relative to many other host species (Robinson et al. 1995), if combined with vigorous defense strategies, might thwart host egg destruction/removal and parasitism.

We used miniature digital video cameras, equipped with infrared illumination that permitted recording in poor light conditions, to document activities of cowbirds at Wood Thrush nests. The objectives of our study were to: (1) identify the manner in which Brown-headed Cowbirds parasitized nests of Wood Thrushes, and (2) observe whether the presence of Wood Thrushes deterred parasitism efforts.

METHODS

We located Wood Thrush nests in nine woodlots, ranging in size from 2 to 24 ha, in the Regional Municipality of Waterloo, Ontario where Wood Thrush studies have been ongoing since 1996 (Friesen et al. 1999, 2005). The woodlots were in an agricultural landscape having 14% forest cover. We began nest searching in mid-May 2006 when Wood Thrushes arrived

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on territory and began nesting, and continued nest searches until mid-August.

We used four miniature infrared video cameras and digital recorder systems (Sentinel ELF™ 24 Digital Video Recording System, Sandpiper Technologies, Inc., Manteca, CA, USA) to simultaneously monitor nests during and after the egg laying period until the nest failed or young were fledged. We deployed cameras at newly built nests where egg-laying had not yet commenced or where the host clutch was not yet complete (2 eggs or less).

Williams and Wood (2002) mounted miniature cameras 30–100 cm from Wood Thrush nest cups and reported an overall nest abandonment rate of 34% due to camera disturbance with higher abandonment rates for nests early in incubation than for nests in later stages. We increased the minimal distance between the camera lens and the nest to 70 cm to minimize desertion with the maximum distance being 100 cm. This allowed a clear view of the nest and its contents, and was less intrusive to the host birds. Each camera was covered in camouflage tape and attached to a similarly camouflaged telescopic pole that was hollow and fitted over an anchoring iron rod. The digital recorder, which operated on a 24-hr basis filming at 25 frames/sec, and accompanying battery were in a camouflaged case ~25 m from the camera. We exchanged digital recorders and batteries daily, and monitored the nest contents at these times using the remote video monitor or manually with a pole and mirror if recording problems had occurred. Recordings from each day were reviewed in the laboratory to document any cowbird activities at the nest site.

OBSERVATIONS

We deployed video cameras at 14 nests from 20 May to 14 July 2006 that were in the early incubation stage. Seven nests were deserted immediately following camera installation. No desertions occurred at any nest ($n = 5$) where cameras were placed on or before 2 June; the average amount of time it took for a female to return to her nest after camera deployment was 2 hrs, 54 min (range = 12 min to 7 hrs, 37 min). Seven of nine nests were deserted when cameras were deployed after 20 June; the average amount of time it took for a female to return to a nest after camera set-up at these later nests was 10 hrs, 15 min.

We documented 10 cowbird visitations to five nests with no parasitism occurring at two other nests where cameras were accepted by the incubating female. Two additional visits by cowbirds to two of the five nests, resulting in the deposition of cowbird eggs, were not recorded because the view was obscured by leaves bent down by drenching rains during the night. All but two of the 10 cowbird visitations occurred early in the morning with a cowbird arriving at a nest between 0528 and 0550 hrs EDT. The two exceptions to this pattern were visits by cowbirds to two nests at 0935 and at 1952 hrs, respectively.

Wood Thrush nests were unattended on six of the 10 cowbird visitations. On each occasion, the cowbirds approached cautiously, hopping from branch to branch before entering the nest. At each of two unattended nests, a cowbird punctured and immediately flew away with a single host egg and returned within 2 min to lay a single egg, taking 21 and 41 sec, respectively, to complete egg laying upon their return. A cowbird visited the first of these nests 3 hrs later in mid-morning, and punctured and consumed the sole remaining host egg in just over 2 min while leaving the cowbird egg intact without adding an egg of its own to the nest. At a third unattended nest, a cowbird removed two eggs in quick succession, dropping one off the side of the nest and flying away with the other in its bill, all in a time span of 24 sec. A cowbird, likely the same one, returned to the nest the following morning to lay an egg when the host female was present.

Female Wood Thrushes were present at the nest on four occasions during a cowbird's visit. The only successful defense of a nest occurred during a brief evening encounter when a Wood Thrush returned to its nest and quickly drove off a cowbird that had hopped onto the nest rim and appeared ready to puncture an egg. The entire episode lasted just several seconds. On three other occasions, cowbirds confronted incubating females. The shortest encounter, beginning at 0550 hrs, lasted 40 sec; the cowbird deliberately approached the nest, circled to the back of the female thrush and flew at her, forcing her to leave the nest into which the cowbird immediately slipped.

The cowbird subsequently received at least 33 pecks and bites to the head and neck from the host female as it sat in the nest yet still managed to puncture a thrush egg and then deposit one of its own. After the cowbird departed, the female Wood Thrush inspected the damaged host egg, removed it, and resumed incubation. A second encounter, beginning at 0539 hrs, spanned 4 min. In this event, a cowbird slowly approached an incubating thrush which flew at the cowbird when the latter was ~0.5 m from the nest, forcing it to withdraw. The cowbird returned within 2 min and elicited a second counter-attack by the thrush which had resumed incubation. The cowbird avoided the thrush and immediately slipped into the nest where it absorbed at least 40 pecks and jabs to the head while it laid an egg. The third and most prolonged encounter, commencing at 0538 hrs, lasted almost 10 min and involved both the male and female Wood Thrush in a spirited defense of their nest. The off-camera battle was so pitched that drifting feathers filled the video screen. The cowbird entered the nest four times during the prolonged struggle and each time was evicted by the thrushes. In one instance, as the cowbird settled into the nest and pumped itself up to deposit an egg, it was struck so forcefully by a diving thrush that it was thrown from the nest, dragging along the entire mat of dark, lining rootlets. Somehow, none of the host eggs were pulled out with the lining. But the cowbird persisted and, on the fifth attempt, slipped into the nest, laying an egg while being pecked repeatedly about the back of the head and neck and rocked so hard by diving host birds that the nest was almost dislodged from its moorings. The thrushes ultimately lost their nest to the cowbird but their resistance prevented the latter from puncturing any of their eggs which it attempted to do on several occasions.

DISCUSSION

Our study revealed that cowbirds parasitize Wood Thrush nests by sneaking into the nests and quickly laying their eggs when host females are absent. But cowbirds also readily use aggressive tactics when host females are present at the nest. Cowbirds are host generalists (Lowther 1993) and it is likely the strategies used to parasitize Wood Thrushes are the same for many other host species.

Parental nest defense from even a relatively large-sized bird such as a Wood Thrush was not an effective deterrent to a challenge by a cowbird. However, the physical costs to cowbirds during these encounters must be considerable because they had to endure a punishing barrage of pecks, jabs, bites, and body blows if they were to prevail at a nest. It is unclear why cowbirds would risk injury to visit a nest when the host was present, given that our video films indicated that female Wood Thrushes invariably leave their nests in early morning to forage, and that cowbirds would have had unimpeded access to nests at these times. Visiting the nest when the host is absent also avoids disturbance that might attract nest predators or result in nest abandonment (Scott 1991).

Video cameras have potential to reveal fascinating and otherwise hard-to-obtain insights into host-cowbird interactions. It is also apparent that cameras can be extremely disruptive to many birds that are being filmed and that nest desertions are common (Thompson et al. 1999, Pietz and Granfors 2000, Williams and Wood 2002). Our study suggests that Wood Thrushes with nests in the early incubation stage will accept the presence of a camera, albeit reluctantly at first, at the outset of the breeding season when their nesting commitment appears to be especially pronounced. However, their tolerance for cameras decreases later in the nesting season. Our desertion rate for cameras installed at nests in the early egg stage from 20 June to 14 July was so high that we abandoned efforts to document cowbird activity at this time. However, we continued to video monitor for possible nest predator activities (i.e., visitations by raptors, corvids, squirrels, etc.) at subsequent nests by modifying our set-up operation. We speculated that late-nesting Wood Thrushes could become habituated to cameras if they were installed ~4 m from the nest site and then moved closer to the nests in daily 1.5 m increments. The cameras were not attached to the video recorders until they were within 1 m of the nest (the maximum recording range for our cameras), which meant that several days elapsed when no filming could occur.

We attempted this procedure from 17 July to 10 August at eight nests, six of which were still at the egg stage when a camera was moved to within 1 m of the nest and when filming could begin. None of the nests was deserted and the average amount of time it took for females to return to the nest after camera set-up at 1 m was 8 min (range = 2–25 min). The strategy of gradually bringing a camera within filming range of a nest causes several days of filming to be sacrificed during which cowbird activity could be missed. The incremental approach can be used to monitor nest predator activity and, if nests are found early in the cycle, can provide valuable information during much of the incubation phase when desertions are most likely to occur if cameras are abruptly introduced at the nest.

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Yellow-breasted Chat and Gray Catbird Productivity in a Fragmented Western Riparian System

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ABSTRACT.—We studied the effects of habitat fragmentation on productivity of Yellow-breasted Chat (*Icteria virens*) and Gray Catbird (*Dumetella carolinensis*) in southern British Columbia in a western riparian ecosystem. Nesting dates were later in isolated habitat patches than in continuous habitat patches for both species. We found no direct evidence that habitat fragmentation decreased productivity in either species. Average fecundity did not significantly differ between continuous (2.54 fledglings for Gray Catbird; 1.78 and 1.67 fledglings for Yellow-breasted Chat in 2002 and 2003, respectively) and isolated sites (1.33 fledglings for Gray Catbird; 1.78 and 0.87 fledglings for Yellow-breasted Chat in 2002 and 2003, respectively). Territory size, as measured by mapping perch locations for breeding adults, was smaller for Yellow-breasted Chats breeding in the Okanagan Valley (0.25 ha) than for chats in mid and high-density southern populations. However, overall fecundity and nest success were similar to more southerly populations. These results suggest that both species can persist in a relatively fragmented ecosystem. *Received 30 June 2005. Accepted 17 October 2006.*

Riparian areas provide critical breeding and stopover habitat for a large diversity of birds. Despite its importance to avian communities, there has been considerable loss of riparian habitat throughout North America (Croonquist and Brooks 1993). Thus, there is a need to understand avian population trends in relation to habitat alteration. Several studies have documented a decrease in productivity and an increase in brood parasitism in association with increased habitat fragmentation (Wilcove and Robinson 1990, Donovan et al. 1995). Under some conditions, habitat fragmentation may lead to a decline in population numbers (Sherry and Holmes 1992, 1993).

Robinson et al. (1995, 2000) documented a relationship between lower productivity and increased habitat fragmentation in eastern forests. Western riparian ecosystems are fragmented by nature because of frequent flooding, ephemeral water sources, and mountainous topography (Hejl 1992, 1994; Ohmart 1994). The few studies that have examined the effects of fragmentation in western landscapes have generally found a less direct relationship between habitat fragmentation and productivity (Tewksbury et al. 1998).

We tested the hypothesis that fragmented habitat negatively affects reproductive success of Yellow-breasted Chat (*Icteria virens*) and Gray Catbird (*Dumetella carolinensis*) in western riparian habitats throughout the Okanagan Valley, British Columbia, Canada. Both species predominantly use wild rose (*Rosa* spp.) as a nesting substrate and forage in close proximity to one another (Cannings et al. 1987; TCM, pers. obs.). Yellow-breasted Chat and Gray Catbird nests are commonly within 5 m of one another. The Okanagan Valley represents the northwest fringe of the Yellow-breasted Chat's breeding range (Eckerle and Thompson 2001), while Gray Catbird populations extend farther north into northern British Columbia (Cimprich and Moore 1995). We compared reproductive parameters for Yellow-breasted Chat with more southerly populations.

METHODS

Aerial photographs of riparian habitat in the Okanagan Valley, British Columbia and Yellow-breasted Chat surveys in 2001 were used to categorize four large riparian patches (15–70 ha) as continuous and five smaller patches as isolated (<2 ha). Continuous sites were tracts of unbroken riparian habitat that con-

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tained >15 ha of unbroken habitat with flowing water. Isolated sites were small fragmented patches of riparian habitat, primarily along roadsides and drainage ditches. Isolated sites were separated from other riparian habitats by >5 km and had ephemeral water sources. All sites were <600 m in elevation and were between the International Boundary (49° 02′ N, 119° 27′ W) and the city of Penticton (49° 30′ N, 119° 35′ W). All study sites were used by chats in 2002. Three of the isolated sites and one continuous site were unused by Yellow-breasted Chats in 2003. Gray Catbird nests were monitored at the same sites as Yellow-breasted Chats in 2003. All sites were monitored for breeding activity between 13 May and 15 August 2002 and 2003.

Surveys for breeding Yellow-breasted Chats and Gray Catbirds were conducted at all sites every 3 weeks to detect breeding pairs and locate nests. We checked nests using mirror-poles or direct observation every 3 days during the nesting cycle to examine clutch size, cowbird parasitism status, hatch date, and nest success or failure (Martin et al. 1997).

Nestlings were measured and banded with a single Canadian Wildlife Service band and three-band color combination at 6 (Yellow-breasted Chat) or 7 (Gray Catbird) days of age. All nestlings were banded between 0700 and 0930 hrs PDT. Adults were captured using passive and target netting techniques. We banded adults with a three-band color combination and an aluminum Canadian Wildlife Service band. All fieldwork was in accordance with Simon Fraser University Animal Care permit 663B-03, bird banding permit 10365 CN, and Canadian Wildlife Service permit 59-03-0426. We used mist nets for up to one-half hr within territories at least 6 m from nests. Locally-recorded species-specific male songs were played for a maximum of 10 min to attract territorial males and females. We also placed passive nets within territories near known flight paths, but did not play tapes to capture some birds.

Daily nest success probability was estimated using maximum likelihood (Hensler and Nichols 1981, Rotella et al. 2000). A nest or female was considered successful if ≥1 Yellow-breasted Chat or Gray Catbird nestling fledged. Female fecundity was calculated as the mean number of fledglings per female per season. All females were single brooded. A second method of calculating fecundity, in which only successful nests were considered, was used for comparison with other studies. Percent parasitism was calculated as the percentage of all monitored nests that contained ≥1 Brown-headed Cowbird (*Molothrus ater*) egg or young at any point during the nesting cycle. Gray Catbirds were omitted from this portion of the study because they reject cowbird eggs.

Spot mapping was conducted for 20 Yellow-breasted Chat territories (5 observations per territory) in 2003. Territory visits were at least 3 days apart and observations were conducted for one-half hr during which all Yellow-breasted Chat sightings were recorded. Observations began 15 min after entering a territory. If a focal bird disappeared for more than 5 min, observations were excluded from the analysis. Time of observation, bird activity, location, perch height, and any other comments pertaining to bird behavior or surrounding ecology were recorded for all sightings. UTM locations were taken after the observation period based on maps and descriptive information recorded during the observation period. Territory size was calculated using Arcview GIS 3.1 area calculator.

We used STATISTICA (Statsoft 2000) for all statistical analysis. One-way analysis of variance (Sanders 1995) was used to test for differences in fecundity, clutch size, territory size, nest initiation, and hatching and fledging dates between years and patch type. Student's *t*-test was used to test for differences in nest success between years. There were between year differences in nest success rate, and the data are presented and analyzed by year. Results were considered significant at $P \leq 0.05$ and are presented as mean ± SD unless otherwise stated.

RESULTS

Twenty-five Yellow-breasted Chat nests were monitored in 2002 while 32 Yellow-breasted Chat nests and 34 Gray Catbird nests were monitored in 2003. Initiation of incubation began the third week of May and continued through 12 July in 2002–2003 for Yellow-breasted Chats and 4 June to 12 July 2003 for Gray Catbirds. Nest incubation, hatching, and fledging dates were later in all years at isolated sites for Yellow-breasted Chats and Gray Catbirds (Table 1).

There were no significant differences in clutch size (3–6 eggs) or number of fledglings between years for Yellow-breasted Chats (Table 1). Percent parasitism ranged from 0 to 44% for Yellow-breasted Chat nests during 2002–2003. There was no difference in fecundity between parasitized and non-parasitized females (2.26 ± 1.53 and 1.71 ± 1.74 fledglings, respectively, t = 1.01, df = 51, P = 0.282). Fifty-seven percent of Yellow-breasted Chat nests monitored fledged at least one nestling in 2002–2003. Similarly, there was no significant difference in either year when clutch size and fecundity of Yellow-breasted Chat females breeding in isolated sites were compared with females in continuous tracts of habitat (Table 1).

Gray Catbird clutch size ranged from two to five and did not differ between isolated (3.67 ± 1.37) and continuous sites (3.76 ± 0.72). Female fecundity of Gray Catbirds in isolated (1.33 ± 1.75) and continuous (2.54 ± 1.65) sites did not differ (t = 0.23, df = 29, P = 0.814; t = 1.84, df = 32, P = 0.075; Table 1). There was no difference in nest success between habitats for Gray Catbird (Table 1).

Yellow-breasted Chat nest success rates differed between years and between continuous and isolated sites. In 2002, nest success was higher in continuous habitats than isolated habitats while in 2003 there was no difference between habitats (Table 1). Nest success was higher in isolated sites in 2003 than in isolated sites in 2002 (Table 1).

Mean Yellow-breasted Chat territory size in 2003 was 0.25 ± 0.24 ha (n = 20). No significant difference in territory size existed between habitat type (0.22 ± 0.28 for isolated sites, 0.29 ± 0.16 for continuous sites; t = −0.56, df = 18, P = 0.584). Territory size was not measured in 2002.

DISCUSSION

We found no evidence that fragmentation or isolation of riparian habitats in a western landscape reduced reproductive success or increased brood parasitism of Yellow-breasted Chats or Gray Catbirds. Percent parasitism, clutch size, and fecundity did not differ be-

TABLE 1. Reproductive characteristics of Yellow-breasted Chats and Gray Catbirds in isolated (< 2 ha) and continuous (> 15 ha) riparian habitat patches in the Okanagan Valley, British Columbia, Canada, 2002–2003. Superscript letters indicate significant differences ($P < 0.05$).

Habitat		Nests	Daily nest success	Percent parasitism	Clutch size	SD	Fecundity (fledglings/female)	SD	Incubation mean date	SD (days)	Hatch mean date	SD (days)	Fledging mean date	SD (days)
Yellow-breasted Chat														
Isolated	2002	9	0.926^{ac}	44	3.75	0.46	1.78	1.79	20 Jun^{d}	11.79	30 Jun^{g}	11.08	18 Jul^{h}	5.32
	2003	8	0.950^{a}	0	3.57	0.53	0.87	0.89	21 Jun^{f}	15.4	3 Jul	12.58	13 Jul	13.25
Continuous	2002	16	1.000^{bc}	12	3.47	1.37	1.78	2.07	7 Jun^{d}	8.61	18 Jun^{g}	8.92	28 Jul^{h}	8.91
	2003	24	0.951^{b}	38	3.37	0.92	1.67	0.92	15 Jun^{f}	13.87	23 Jun	12.45	4 Jul	15.59
Gray Catbird														
Isolated	2003	6	0.916	0	3.67	1.37	1.33	1.75	27 Jun	7.94	9 Jul	9.74	23 Jul	8.72
Continuous	2003	28	0.914	0	3.76	0.72	2.54	1.65	16 Jun	10.96	28 Jun	11.34	9 Jul	11.41

tween isolated and continuous habitat patches for either species. However, delayed incubation at isolated sites by both species suggests continuous sites may be preferred habitat, filling up sooner and causing late arrivals to breed elsewhere (Fretwell and Lucas 1970). Differences between years may reflect local environmental fluctuations. More breeding pairs were detected in 2003 but decreased nest success in 2002 may be indicative of overall decreased habitat quality in that year.

Both Gray Catbirds and Yellow-breasted Chats had similar patterns of productivity and nest success between habitats in 2003. When compared to other Yellow-breasted Chat populations breeding at the core of their range (Thompson and Nolan 1973, Schadd and Ritchison 1998, Rickets and Ritchison 2000), the Okanagan population had similar levels of productivity.

Yellow-breasted Chat territory size (0.25 ha) in the Okanagan Valley was smaller than reported for mid and high-density southern Yellow-breasted Chat populations (0.5–1.0 ha, Dennis 1958; 1.24 ha, Thompson and Nolan 1973). Clutch size in the Okanagan (3.5 eggs/nest) was the same as that of more southerly populations (3.5 eggs/nest; Thompson and Nolan 1973). Overall fecundity (2.86 young/successful nest) was within the range of that reported for southeastern populations (3.25 young/successful nest, Schadd and Ritchison 1998; 2.3–2.9 young/successful parasitized and non-parasitized nests, Whitehead et al. 2000). The percentage of nests that were successful (57%) was midrange when compared to other studies (22.5%, Thompson and Nolan 1973; 84.2%, Schadd and Ritchison 1998; 45%, Rickets and Ritchison 2000). The consistency of fecundity values between the Okanagan Valley and southern populations indicates conditions at the fringe of this species range are not negatively affecting productivity.

Despite the narrow range in latitude for all sites monitored, later nest initiation and fledging dates were found in isolated riparian patches. Consequently, we expected birds breeding in this habitat to have reduced nest success or fecundity. The absence of a significant difference in fecundity between isolated riparian patches and large tracts of habitat indicates Yellow-breasted Chats and Gray Catbirds can successfully reproduce in a highly fragmented environment. Settlement patterns in this study suggest that, although continuous and isolated sites may be comparable in quality, continuous tracts may be preferred breeding locations and have the capability to support higher breeding densities. Alternatively, isolated patches may lag behind continuous patches in resource availability for reproduction. It is also possible that continuous patches may cater to the semi-colonial nature thought to be a characteristic of Yellow-breasted Chats (Griscom 1923).

The current level of riparian habitat fragmentation does not appear to be a limiting factor for either Yellow-breasted Chat or Gray Catbird populations in the Okanagan Valley, British Columbia. Parameters for Yellow-breasted Chat breeding at the northwest extent of their range are comparable to more southerly populations, suggesting that conditions at the edge of the species' range do not reduce productivity. The smaller territory size of Yellow-breasted Chats in the Okanagan Valley may suggest a higher concentration of breeding resources.

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Documentation of a Polygynous Gray Catbird

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ABSTRACT.—Polygyny occasionally occurs in passerine species that are generally socially monogamous. We document the second case of polygynous mating in the Gray Catbird (*Dumetella carolinensis*) and provide the first detailed account of this behavior. Daily provisioning rates of the polygynous male documented this male provisioned one nest more than the other (5.9 ± 2.2 trips/hr vs. 1.7 ± 1.1 trips/hr). The difference between the male's provisioning rates diminished when standardized for the number of chicks per nest. Polygyny appears to be an alternative mating strategy for the Gray Catbird in certain situations. *Received 5 July 2006. Accepted 19 November 2006.*

Polygyny is a mating system in which a single male forms long lasting breeding associations with more than one female at the same time (Searcy and Yasukawa 1989) and is uncommon in birds (Alatalo et al. 1981). Where polygyny does occur in birds, it is generally in only a subset of a population, with most individuals exhibiting social monogamy (Secunda and Sherry 1991, Ford 1996). Seventy-one species of passerine birds (26%) within the United Sates and Canada have been reported to exhibit some form of polygyny (Ford 1996). The polygyny threshold model (PTM) stipulates that females should only engage in polygynous mating if the benefit of mating with an already mated male outweighs the costs associated with such a mating (Verner 1964, Verner and Willson 1966). An alternative to the PTM is the "deception hypothesis" (von Haartman 1951, 1956; Alatalo et al. 1981). The mating status of the polygynous male under the deception hypothesis is unknown to females mating with him because the male is polyterritorial and possesses two territories usually separated by territories of other males (Alatalo et al. 1981). The cost to females associated with this form of polygyny is not compensated.

In either the polygyny threshold model or the deception model, secondary females have a greater cost than primary females and the most likely cost is reduction in male parental care. However, polygyny is not always costly for a female. Possible benefits include mating with a genetically superior male, having access to a high quality territory, nest protection, and enhancement of foraging success, which are applicable only when the polygynous mates share a single territory. Polyterritoriality has been reported for only 11 of the 71 North American passerines known to practice polygyny (Ford 1996).

The Gray Catbird (*Dumetella carolinensis*) is a common monomorphic North American songbird that exhibits bi-parental care, and is believed to be both genetically and socially monogamous. The male contributes most of the nestling feeding during the early nestling period, while the female does most of the brooding. However, the Gray Catbird may not always be monogamous. Johnson and Best (1980) reported the only known case of a single male catbird tending two nests. Few details of this observation were documented. In that particular instance there was one competing territory between the two nests. We document another such case in the Gray Catbird in this paper.

METHODS

We conducted observations during a study of paternal care of the Gray Catbird in East Buffalo Township, Pennsylvania (40° 59′ N, 76° 56′ W). The study site is 24 ha and is comprised of forested, grassy, and edge habitat. Twenty-five male and 13 female Gray Catbirds were mist netted and banded with U.S. Government metal bands and unique color combinations before the laying period. Body condition measurements (100 ×

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[mass^{-3}/tarsus length]) and blood samples were taken for each bird. We monitored the fate of Gray Catbird nests and made daily measures of paternal effort through approximately 1.5 hrs of observations of provisioning using digital video cameras (Sony DCR-TRV22) positioned approximately 1.5 m from the nests. Gray Catbirds acclimate relatively quickly to this type of camera at this distance (Dolby et al. 2005). Each nest used was observed at least 4 days during the nestling period.

The two nests discussed in this paper (#50 and #78) were cared for by the same male, and were filmed seven and six times, respectively. Five video observations were included for both nests from 31 July to 4 August between 1000 and 1400 hrs EDT. Observations of the two nests were not entirely synchronous and the video records were truncated to include only overlapping times to facilitate comparison of differences in paternal investment between the two nests. The data are presented as means ± SD.

RESULTS

A male Gray Catbird (#433) was banded on 23 May 2005 and his body condition measurements were taken. This male had a body condition score (6.2×10^{-5}) lower than the population average ($7.3 \times 10^{-5} \pm 2.0 \times 10^{-5}$). He aggressively guarded two nests (#50 and #78 with respective clutch sizes of 3 and 2), 69.5 m apart. These nests were in an area which appeared to have the highest amount of shrub, thorny, and fruiting species within the study site. There appeared to be a high density of catbirds in this general area but we did not detect an active intermediate territory. All eggs in both nests hatched. On 28 July two eggs had hatched in both nest #50 and nest #78. The following morning an additional egg hatched in nest #50.

The frequency of male provisioning visits was higher at nest #50 (5.9 ± 2.2 trips/hr) than at nest #78 (1.7 ± 1.1 trips/hr). This difference could be a result of the difference in brood size between these nests. The difference between the two nests diminished after standardizing for brood size. However, the frequency of male provisioning visits was still higher at nest #50 (1.9 ± 0.8 trips/hr) than at nest #78 (0.8 ± 0.5 trips/hr) (Fig. 1).

DISCUSSION

Polygynous mating is known to occur in some passerine birds (Searcy and Yasukawa 1989, Ford 1996) but typically does not occur in Gray Catbirds (Cimprich and Moore 1995). Gray Catbirds have a high level of male care (Slack 1976, Cimprich and Moore 1995) and polygyny would not be expected to occur through female choice unless male or territory quality is sufficiently variable (Verner 1964, Verner and Willson 1966, Temrin 1984). However, females may not recognize the prior mating status of males in all polygynous matings (Alatalo et al. 1981). Although polygyny is unexpected in this species, under the polygyny threshold model, one may predict that a female Gray Catbird would prefer to mate with an already mated male if he was of higher quality than other males. However, our measurement of body condition for male #433 was within one standard deviation of the mean.

The synchrony and proximity of the two nests make it less likely the two females paired with the same male without detecting each other; if the females knowingly chose to settle polygynously, the benefits of pairing with this particular male should outweigh the cost of being polygynous. Johnson and Best (1980) reported the nests they observed were further apart (160 m) and the clutches were laid asynchronously. This fits the polyterritorial deception model better than our example. These separate cases of polygyny present the possibility of multiple breeding strategies in Gray Catbirds. Male #433 appeared to provide similar care for his nests when standardized for brood size, contrasting with polyterritoriality and the predictions of deceptive polygyny (Smith et al. 1982, Secunda and Sherry 1991).

It has been accepted that the Gray Catbird is socially monogamous and it is now evident there are situations when some birds mate polygynously. Future studies should consider the reproductive strategies of this species.

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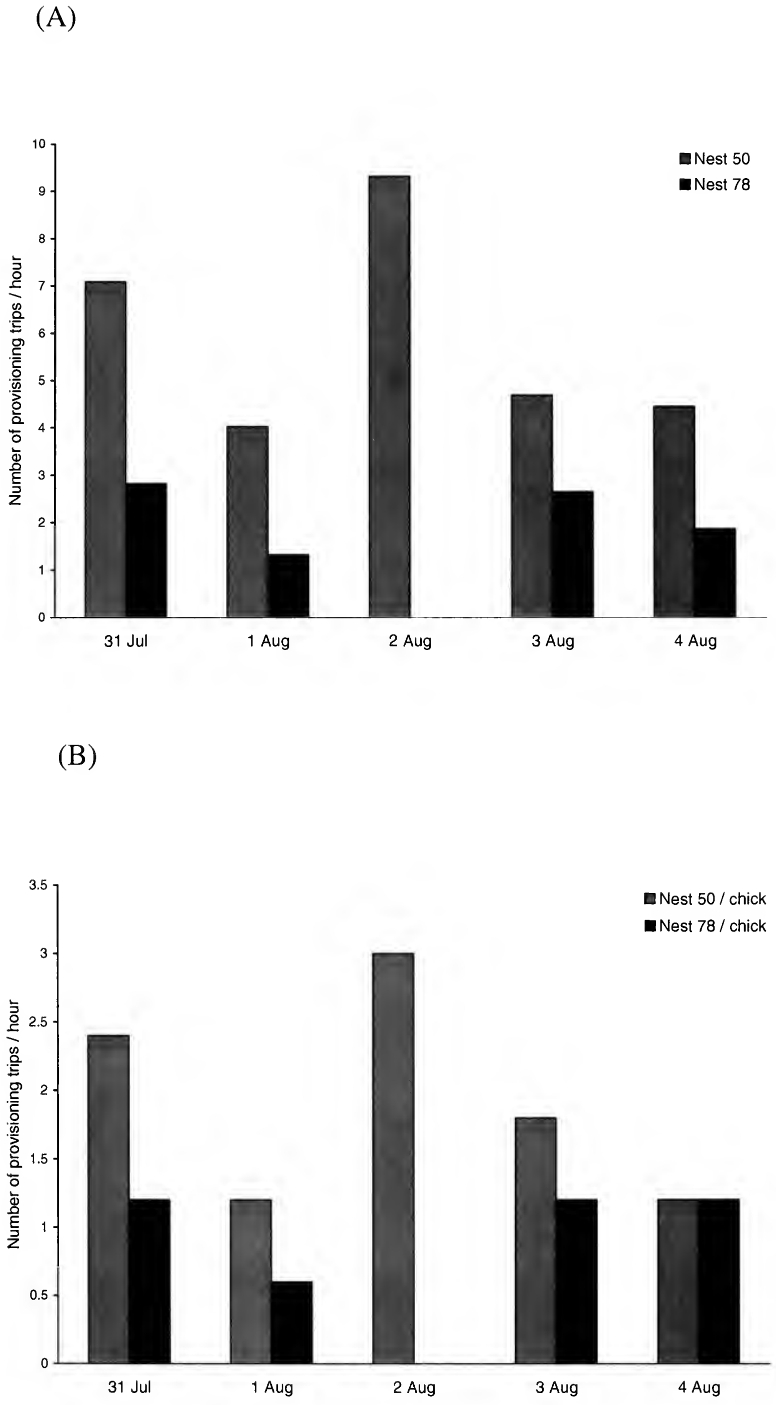

FIG. 1. (A) Number of daily provisioning trips/hr to each of two nests tended by the same male Gray Catbird and (B) the number of daily provisioning trips/hr standardized for number of nestlings.

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Rockhopper and Macaroni Penguin Colonies Absent from Isla Recalada, Chile

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ABSTRACT.—Macaroni (*Eudyptes chrysolophus*) and Southern Rockhopper penguins (*E. c. chrysocome*) have been classified as Vulnerable due to decreasing populations in recent decades. We report on a survey of Isla Recalada, Chile, a site described historically as containing an estimated population of 10,013 (±570) Rockhopper and 559 Macaroni penguins. Our survey was conducted on 14 and 15 November 2005 to coincide with peak colony attendance. No Rockhopper or Macaroni penguins were observed on Isla Recalada during this period. This survey suggests the population of these penguins has dispersed due to possible anthropogenic pressures or climate variation, and that both species of penguins have been extirpated from Isla Recalada. *Received 26 July 2006. Accepted 4 December 2006.*

The Southern Rockhopper Penguin (*Eudyptes c. chrysocome*) and Macaroni Penguin (*Eudyptes chrysolophus*) along the coast of Chile are restricted to the southern islands with estimated populations of 75,000–150,000 and 25,000–75,000 individuals, respectively (Schlatter 1984, Woehler 1993). Both taxa have been classified as Vulnerable by the IUCN/BirdLife International Red List (BirdLife International 2004) because of declining populations of at least 30% over the last 30 years and continued anthropogenic pressures (e.g., fisheries activities) and changes in the marine environment.

Breeding sites for Southern Rockhopper Penguins are restricted mostly to the islands

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TABLE 1. Survey of Rockhopper and Macaroni penguins at Isla Recalada, Chile, 1989–91 and 2005.

	1989	1990	1991	2005
Rockhopper Penguin	10,013	6,777	3,304	0
Macaroni Penguin	599	421	0	0

off southern Chilean fiords between 47° and 56° S (Williams 1995) with egg production occurring from November to early December. The world population estimate for this subspecies has been placed at 475,000 breeding pairs at 51 sites (Bingham and Mejias 1999). Recent surveys indicate a population of 272,000 breeding pairs occurs on the Falkland Islands. These same surveys suggest the Falkland Island population has been stable since the mid 1990s, but has declined from 1.4–1.8 million pairs, a decline of over 80%, since the initial surveys in 1932/33 (Clausen and Huin 2003, Pütz et al. 2003). Recent surveys in Argentina involving the inventory of 180,000 pairs of Rockhopper Penguins on Staten Island indicate numbers have dramatically increased from a few thousand pairs to 167,000 pairs at Bahía Franklin and may indicate a shift of birds from the Falkland Islands (Schiavini 2000).

The number of Southern Rockhoppers in Chile was estimated to be 175,000 pairs with the largest colonies of 70,000 and 13,000 pairs on Isla Noir and Diego Ramirez Islands, respectively. However, there is no comprehensive program to monitor long-term population trends (Venegas 1984, 1991; Woehler 1993). The colony of 70,000 pairs on Isla Noir was estimated to contain 35% of the total number along the coast of Chile (Venegas 1998). Six colonies of Southern Rockhopper Penguins and three colonies of Macaroni Penguins have been described on Isla Recalada, Chile (74° 20′ S, 53° 17′ W).

The overall objective of our survey was to gather and summarize data on Southern Rockhopper and Macaroni penguins, based on breeding pairs, obtained during an assessment of coastal islands from Isla Noir (54° 20′ S, 73° 10′ W) to Isla Recalada (Fig. 1). This paper reports on the absence of these two penguins from Isla Recalada.

METHODS

We surveyed known locations of the Rockhopper and Macaroni penguin colonies on Isla Recalada on 14 and 15 November 2005 using maps and Global Positioning Satellite (GPS) coordinates from previous studies. Four investigators, using stratified random sampling techniques, conducted land-based systematic sampling of all geographic areas known to be used by penguins as described by Venegas (1984, 1991, 1998), Soto (1990), and Venegas and Soto (1992). The goal was to collect data from each colony site to estimate total penguin population size. We also used coastal searches by boat, based on historic data for reference, to expand the survey. Study sites on Isla Noir and Leonard Island (74° 04′ W, 53° 23′ S), the latter 4 nautical miles southeast of Isla Recalada, demonstrated that timing of our survey coincided with peak colony attendance for the two species (MM and DAO, unpubl. data).

RESULTS

No active nest sites or individual crested penguins were found in any of the Rockhopper or Macaroni penguin colonies on Isla Recalada in 2005. Evidence of historic nesting colonies was present with clearly defined paths and remnants of individual nest cups within areas of tussock grasses. Active burrows, excavated by nesting Magellanic Penguins (*Spheniscus magellanicus*) were present within the former Rockhopper Penguin colonies within 50–100 m of the shoreline. Recent tracks and guano were evident in areas only associated with Magellanic Penguin nests.

DISCUSSION

No Rockhopper or Macaroni penguins were observed in 2005 within historical breeding colonies on Isla Recalada. Venegas and Soto (1992) abandoned efforts to survey the area in 1992 due to poor weather conditions. Suitable nesting areas, primarily tussock grasses, remained in 2005 with little or no evidence of recent human activities.

Surveys of penguin colonies on Isla Recalada documented a decline in Rockhopper Penguin colonies from 1989 to 1991; 10,013 (±570) to 3,304 (Soto 1990, Venegas 1991, Venegas and Soto 1992). Macaroni Penguins declined from 559 in 1989 to 421 in 1990

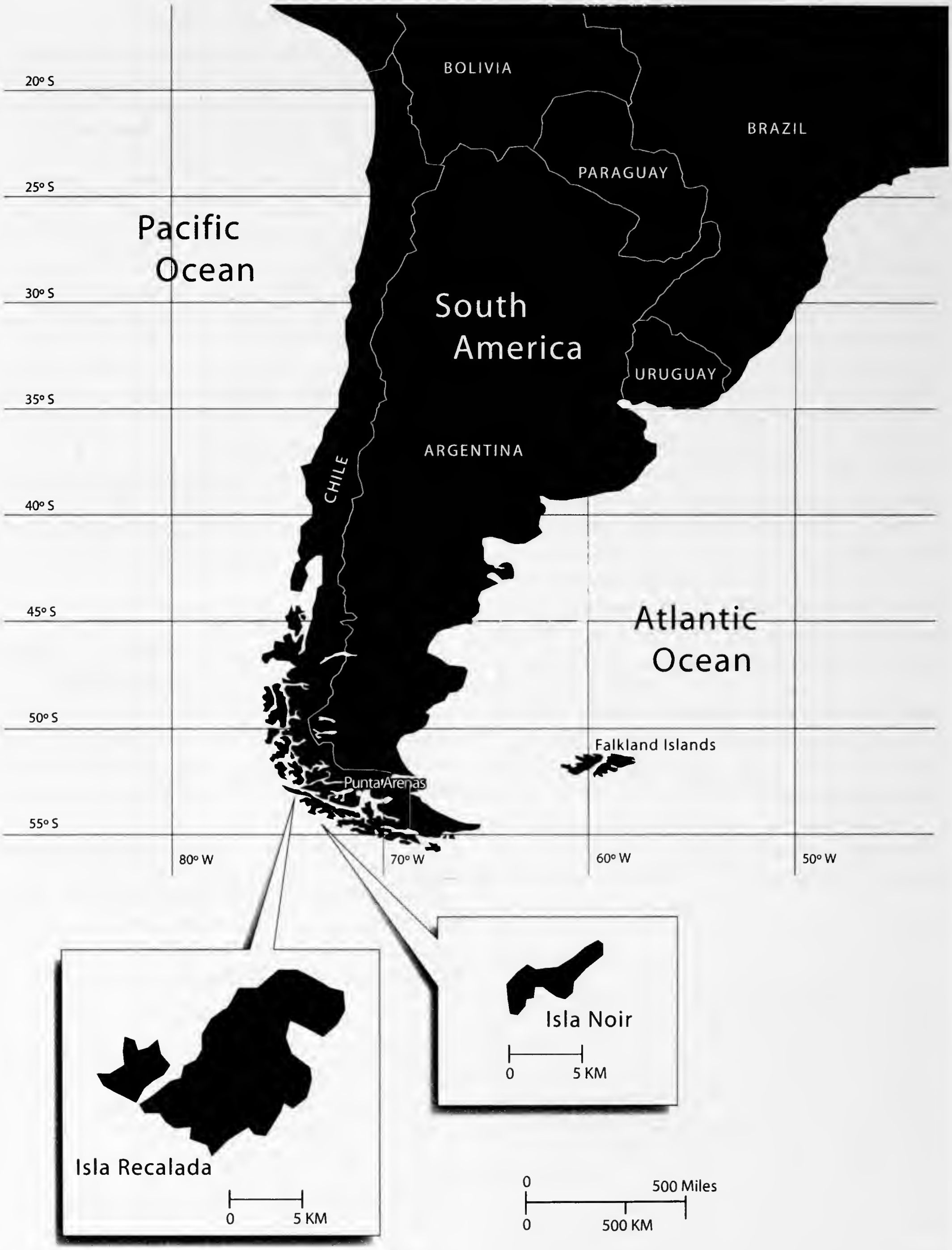

FIG. 1. Isla Noir and Isla Recalada along the coast of Chile.

with no Macaroni Penguins observed within these colonies in 1991 (Soto 1990, Venegas 1991, Venegas and Soto 1992). The number of active nests within the Rockhopper Penguin colonies also demonstrated a marked decline, e.g., colony #5 had 602 active nests in 1989 and 68 nests in 1991 while colony #1 had 135 nests in 1991 versus 739 during the 1989 season (Venegas and Soto 1992).

One possible explanation for this decline is collection of adult penguins for export to zoological parks from 1984 to 1992. These activities, which probably created a disturbance within the breeding colonies, may have caused adult penguins to move to other colonies (Venegas 1991, Venegas and Soto 1992). Interviews with local fishermen revealed that from 1992 to 1997, shortages of fish-based bait for crab pots led some fishermen to sites such as Isla Recalada to procure alternative sources of bait, including adult penguins.

El Niño Southern Oscillation (ENSO) events, particularly in 1996–97, may have had a role in altering prey availability, although the effects of these events were greatest between 5° and 15° S (Shaffer et al. 1999). The 1996–97 ENSO event was the strongest in modern history and resulted in a decline in Humboldt Penguins (*Spheniscus humboldti*) (BirdLife International 2003, Paredes et al. 2003). Warming of ocean temperatures during ENSO events may result in lower annual production within penguin colonies (Fortescue 1999, Taylor et al. 2004).

Monitoring of penguin colonies must continue to be implemented along the coast of Chile to estimate population size, status, and population trends. These efforts will allow for implementation of conservation efforts within specific areas involving important penguin populations during possible shifts in populations due to prey availability and detrimental anthropogenic activities. There is a need to immediately establish procedures and to control collecting expeditions as suggested by Venegas (1991).

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Nocturnal Migrants Foraging at Night by Artificial Light

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ABSTRACT.—Artificial lights can have detrimental effects on nocturnal migrant birds and other wildlife, yet some species of typically diurnal insectivorous birds are capable of foraging at night under artificial illumination. Here, we report observations of at least 15 wood-warbler species (Parulidae), one tyrant-flycatcher (Tyrannidae), and one mimid (Mimidae) foraging at night in areas illuminated by powerful artificial lights. To our knowledge, our observations represent the first report of a mixed-species flock of birds foraging on insects attracted to artificial lights or within foliage illuminated by artificial lights at night. *Received 2 October 2006. Accepted 14 December 2006.*

Artificial light sources can have negative effects on birds and other animals (Le Corre et al. 2002, Bird et al. 2004, Rich and Longcore 2006). However, some diurnal bird species are capable of using artificial lighting to forage at night. Here, we report observations of at least 15 wood-warbler species (Parulidae), one tyrant-flycatcher (Tyrannidae), and one mimid (Mimidae) foraging at night in areas illuminated by powerful artificial lights.

METHODS

MGH and TCL noticed a large number of flight calls at 2130 hrs EST on 11 October 2005 near the house of MGH, ~1 km from Schoellkopf Field within Cornell University's football stadium in Ithaca, New York (42° 26′ N, 76° 26′ W). MGH and TCL contacted additional observers and about a dozen people gathered at the stadium. Powerful artificial lights (156 1,500-watt metal halide bulbs mounted in 2 groups of 30 bulbs and 4 groups of 24 bulbs) illuminated the stadium following an evening athletic practice and for the duration of our observations. We recorded observations within and along the periphery of the stadium until the lights were turned off shortly before 0200 hrs on 12 October 2005. The group searched the stadium area with individuals or small groups of observers at times separating to cover different areas simultaneously. Winds conducive to migration occurred across much of the northeastern United States during this period and several days prior, while a stalled cold front caused light precip-

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itation during the night of observation (Dinsmore and Farnsworth 2006).

OBSERVATIONS

We heard thousands of migrants calling from inside the stadium, creating a constant background noise of bird calls. These calls came from birds flying low overhead and birds that had landed in and around the stadium. Near the start of observations, MGH and TCL counted 26 flight calls belonging to a variety of species in one 10-sec period (extrapolated to 156 calls/min). Numbers for each species (Dinsmore and Farnsworth 2006: 16 [Table 1]) were difficult to estimate because of apparent high call rates and the potential for double-counting circling birds. Large numbers of Savannah Sparrows (*Passerculus sandwichensis*), Yellow-rumped Warblers (*Dendroica coronata*), and other migrants were immediately apparent. Some species actively foraged among the foliage of illuminated trees and a few species sallied into the air to capture insects attracted to or disoriented in the stadium lights. Most insects pursued were moths, although birds also captured non-Lepidoptera. A Gray Catbird (*Dumetella carolinensis*) made one long ~10 m sally to hawk an insect from the air under a stadium light. Both Eastern Phoebe (*Sayornis phoebe*) and Nashville Warbler (*Vermivora ruficapilla*) were observed by MJA sallying after moths. Northern Parula (*Parula americana*), Blackburnian (*Dendroica fusca*), and Palm warblers (*D. palmarum*) searched for food among the foliage of illuminated trees. Black-and-white Warblers (*Mniotilta varia*) foraged creeping along large branches of illuminated trees and Common Yellowthroats (*Geothlypis trichas*) foraged among the foliage of lower bushes, but also frequently perched higher in the canopy of trees with other birds. Black-throated Blue (*Dendroica caerulescens*), Black-throated Green (*D. virens*), and Bay-breasted warblers (*D. castanea*) made aerial sallies after insects and appeared to glean insects from foliage. Yellow-rumped Warblers and American Redstarts (*Setophaga ruticilla*) were seen mainly using aerial sally maneuvers to take insects from foliage or the air. We suspected that six other wood-warbler species, including Ovenbird (*Seiurus aurocapillus*), Tennessee (*Vermivora peregrina*), Chestnut-sided (*Dendroica pensylvanica*), Magnolia (*D. magnolia*), Blackpoll (*D. striata*), and Hooded warblers (*Wilsonia citrina*), were also foraging by artificial light but could not confirm these behaviors. Many individuals and species of warblers foraged simultaneously within the same trees interacting with each other as is typical in mixed-species flocks during daytime. We did not observe foraging behavior in less insectivorous species such as Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Savannah Sparrows. These species simply perched in trees, on bleachers, or on the artificial turf field. A single Red-tailed Hawk (*Buteo jamaicensis*) perched on the roof above the stadium and made at least one flight across the stadium. However, we could not confirm whether this bird attempted to attack potential prey or attempted to hunt nocturnally within the artificially illuminated area.

DISCUSSION

To our knowledge, this is the first report of a mixed-species flock of diurnal insectivorous birds actively foraging both in artificially illuminated vegetation and on insects attracted to artificial light sources. We observed additional events of mixed-species warbler flocks foraging late at night under the artificial lights at this location during 29 August and 15–16 September 2006 including light-aided nocturnal foraging among Yellow (*Dendroica petechia*), Magnolia, Blackpoll, and Cape May warblers (*D. tigrina*) sallying from the top of an illuminated conifer. Our observations may also represent the first examples of artificial light-aided nocturnal foraging for all species reported here except Gray Catbird, American Redstart, and Eastern Phoebe (Latham 1936; Bakken and Bakken 1977; Robert DeCandido, pers. comm.).

We suspect the lights caused problems for birds orienting in the sky, but most of the birds appeared to have no trouble orienting in trees and near the ground below the lights. We observed few mortalities during 11–12 October 2005, although one dead Ovenbird and one dead female Black-throated Blue Warbler were recovered from the stadium and nearby buildings. We captured four Common Yellowthroats trapped in open lit doorways and released them away from buildings after the stadium lights were turned off. We were surprised that we encountered relatively few thrushes on or near the ground, despite the number and diversity of flight-calls from thrushes passing overhead. We are unable to explain why few thrushes landed during this event while so many warblers and other species were grounded.

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Yellow-throated and Red-eyed Vireos Foraging on Green Anoles During Migration

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ABSTRACT.—Yellow-throated (*Vireo flavifrons*) and Red-eyed vireos (*V. olivaceus*) were observed feeding on green anoles (*Anolis carolinensis carolinensis*) at two localities in Florida and one in South Carolina. Vireos are long-distance migrants that require foods high in fatty acid content, especially when engaging in migration. It is not unlikely that vireos have an opportunistic foraging strategy to obtain the necessary food requirements, including attacking and consuming prey items such as small lizards. This note provides the first published reports of lizards taken as prey by these two species. *Received 24 November 2006. Accepted 20 March 2007.*

The diets of North American vireos have been well described (Chapin 1925, Tyler 1950, Williamson 1971, Graber et al. 1985, Ridgely and Tudor 1989, Rodewald and James 1996, Cimprich et al. 2000). The diet of the Yellow-throated Vireo (*Vireo flavifrons*), based upon analysis of 160 stomachs from specimens collected from April through September in breeding areas throughout North America, consists of 98.3% animal matter and 1.7% plant material (including small fruits and seeds). Insects (Insecta; eggs, instars, and adults of at least five Orders) comprise 95.8% of the animal food with the remainder being spiders (Arachnida) 2.4% and small snails (Mollusca) 0.06% (Chapin 1925). Butterflies and moths (Lepidoptera) accounted for 42%+ of the insects taken and vegetable matter was primarily consumed in fall and winter (Chapin 1925, Rodewald and James 1996). The diet of the Red-eyed Vireo (*Vireo olivaceus*) has been summarized by Chapin (1925), Tyler (1950), and more recently by Cimprich et al. (2000). Food items consist of insects (Insecta; eggs, instars, and adults of at least eight Orders), spiders (Arachnida), small snails (Mollusca), a large variety of small fruits, and occasion-

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ally flowers and leaf buds (Chapin 1925, Cimprich et al. 2000). Contents of 569 stomachs (Apr–Oct) within the breeding range included 85% animal matter and 15% plant material (Chapin 1925). Small fruits were most frequently taken in late summer and fall in breeding areas (Chapin 1925, Tyler 1950, Williamson 1971, Graber et al. 1985). The species is almost entirely frugivorous while wintering in northern South America (Ridgely and Tudor 1989).

Vireos kill larger prey by crushing, shaking vigorously, or beating against a branch (Southern 1958, Rodewald and James 1996). Smaller prey is swallowed whole. Larger prey are held with a foot against a branch and eaten piecemeal (Williamson 1971, Rodewald and James 1996). The objective of our paper is to report two species of vireos feeding on *Anolis* lizards during migration in South Carolina and Florida, USA.

OBSERVATIONS

On 21 September 2006, while searching for neotropical migrants in the maritime forest at Myrtle Beach State Park, Horry County, South Carolina, PWS observed an adult Red-eyed Vireo feeding on a brown-colored green anole (*Anolis carolinensis carolinensis*). This abundant small arboreal lizard has: (1) the ability to change color (green to brown and vice versa), (2) a wide range in the southeastern United States, and (3) attains a length up to 19 cm, 60–65% of this length being the tail (Conant 1958). The bird had apparently just captured the anole, ~ 12–13 cm in length and still limp, but the event was not witnessed. The bird held the lizard with its left foot against a branch and was steadily pecking the head, removing and swallowing small pieces of tissue. PWS watched this procedure for 15+ min with binoculars at an estimated 6 m with the bird clearly illuminated in direct sunlight. The bird was perched in a sweetgum (*Liquidambar styraciflua*) at a height of 5 m. The body and head of the anole were still intact, further indicating recent capture. When the vireo changed position on the branch, it continued to hold the anole with its left foot. When PWS left the site, the vireo was still actively feeding on the anole.

LSA and RLP observed a migrant Yellow-throated Vireo eating a green anole at 0900 hrs EDT at Key West, Monroe County, Florida on 13 April 1987. The vireo, perched in a strangler fig (*Ficus aurea*), was observed feeding on the lizard for 35 min. It first pulled pieces of flesh from the head, eating the eyes and what appeared to be the brain. After tearing the remains of the head from the body and dropping the head to the ground, the bird fed on the tissue of the neck region. The vireo bit off the legs and tail, and discarded them while feeding on the anole's abdomen. LSA later watched a migrant Red-eyed Vireo for 5+ min at 7 m eating a green anole at Ft. DeSoto County Park (Mullet Key), Pinellas County, Florida in mid morning on 27 April 1987. The bird was perched 3 m above ground in a woman's tongue tree (*Albizia lebbeck*).

DISCUSSION

These appear to be the first reports of Yellow-throated and Red-eyed vireos feeding on lizards; literature searches did not reveal reptiles or amphibians having been reported taken by these two species. There is a record of a White-eyed Vireo (*Vireo griseus*) feeding on a small *Anolis* (Chapin 1925, Hopp et al. 1995). This appears to be the only previously published account of a vireo feeding on a lizard. Prior to the 1987 observations, the late Larry Hopkins (pers. comm., with LSA) reported watching a migrant Yellow-throated Vireo feeding on an introduced Cuban brown anole (*Anolis sagrei sagrei*) (Conant 1958) at Ft. DeSoto County Park, Pinellas County, Florida. All three vireos are long-distance migrants that possess the ability to greatly increase fat stores in preparation for migration (i.e., become hyperphagic), especially before a trans-Gulf flight (Moore et al. 1995). The energetic costs of migration require high levels of fatty acid in the diet of Red-eyed Vireos (Pierce and McWilliams 2005). Moreover, numerous nutritional requirements of individual vireos during the breeding season (Pierce et al. 2004, Pierce and McWilliams 2005) likely result in these species exhibiting opportunistic foraging behavior. Vireos are almost completely insectivorous requiring at least 75–85% animal matter in their diets (Cimprich et al. 2000, Pierce and McWilliams 2005). Red-eyed Vireos in laboratory tests routinely chose diets with higher fatty acid content (Cimprich et al. 2000, Pierce et al. 2004). Thus, it is likely that vireos will attack and consume numerous animal species, including small lizards, when the opportunity arises.

Two of the vireos we observed (Apr) were in migration. One vireo observed (Sep), was likely preparing for migration to wintering areas in South America. It is likely the three birds were in an energetic state that required a highly nutritious food resource. Vireos are known to be opportunistic foragers during migration (Woodrey and Moore 1997). It is possible that at least the two species of vireos we observed take small lizards as prey with greater frequency than current evidence indicates. We did not observe captures of the lizards by the vireos and do not know the specifics as to how vireos actually obtained these prey, the physical condition of the prey at time of capture, or other circumstances involved.

Recent accounts of other small insect-eating birds taking small vertebrate prey include: (1) a migrant Summer Tanager (*Piranga rubra*) at Horn Island off the coast of Mississippi on 3 April 1993 eating a green anole (Aborn and Froehlich 1995), and (2) a House Wren (*Troglodytes aedon*) eating a juvenile house gecko (*Hemidactylus frenatus*) in Golfito, Costa Rica on 22 May 2002 (Barquero and Hilje 2005).

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Once Upon a Time in American Ornithology

The "*Codex canadiensis*" (*Codex*) was completed in manuscript by Jesuit missionary Father Louis Nicolas (1634–ca. 1678) sometime after 1675 apparently as part of or a companion to a larger work known as "*Histoire naturelle des Indes Occidentalis*" (*Histoire*, "Natural History of the West Indies"). Nicolas is little known today and his opus is yet to be translated from its original French into English. So what do we know of the manuscript itself, the author, and its perpetuation? Each of these three components and their inter-relationships are fragmented and sometimes uncertain (Reeves, H. M., F.-M. Gagnon, and C. S. Houston. 2004. "*Codex canadensis*", an early manuscript of Canadian natural history. *Archives of Natural History* 31:150–166).

The *Codex* is in the custody of the Gilcrease Museum, Tulsa, Oklahoma, and a photographic copy resides in the National Archives of Canada, Ottawa, Ontario. It consists of 79 leaves with 182 illustrations. The paper is large, heavy parchment stitched on the fold, and bound in fine red morocco with gilt printing and ornamentation, all in remarkably good condition. The entire work was penned in iron gall (sepia) ink, and some figures are lightly washed in red, yellow, brown, or blue. The *Codex* lacks a title page, evidence of its creator, and running text other than in the introduction; however, some illustrations bear names, numbers, or short captions. The last 53 pages depict approximately 53 birds, 67 mammals, 33 fishes, ~10 reptiles, batrachians, and insects, plus 18 plants.

Some believe the manuscript to have been once in the possession of Louis XIV before vanishing for more than two and one-half centuries, and then emerging in 1930 in the hands of Baron Marc de Villiers, and published by him in an uncolored facsimile edition of 110 copies. Two inferior Canadian editions, incorrectly attributed to authorship, followed.

Louis Nicolas was born in Aubenois, Ardeche, Province of Toulouse, France, on 24 August 1634. After studying philosophy for 2 years, he entered the Company of Jesus on 16 September 1654. Following further religious preparation, Nicolas, in 1661, expressed a desire to be sent to New France (Canada) to undertake missionary work. His request was eventually granted and on 25 May 1664 he arrived in Quebéc. From there, he undertook proselytizing efforts on behalf of Catholicism among as many as 15 Indian tribes of the vast upper St. Lawrence and the Great Lakes region during 1664–1675. For a missionary, Nicolas sometimes displayed unconventional and unbecoming traits, and in 1675 he returned to France, only to become further estranged from the Jesuit Order. He abandoned it and was defrocked in 1678.

Several Francophone scholars contributed to the unraveling of the *Histoire* and to a lesser extent, the *Codex*. They include François-Marc Gagnon (1987), Anne-Marie Blouin-Sioui (1979, 1981), Dorothée Sainte-Marie (1980), André Vachon (1982), Guy Tremblay (1983), and particularly Germaine Warkentin. Noting similarities between the figures in the *Codex* and the descriptive text of the *Histoire*, Gagnon, a visual arts historian, concluded the former had once been part of the latter. How the two became separated and precisely how the *Codex* ended in the possession of the agent, possibly Henry Stevens, Son, & Stiles, London, from whom the Thomas Gilcrease Foundation purchased it, are unknown.

And what of Thomas Gilcrease himself? Thomas was born on 8 February 1890, in eastern Oklahoma, the eldest of 14 children in a family of modest means. Because of his one-eighth Muskogee (Creek) blood, he and his siblings were each allotted a quarter-section (160 acres [64.752 ha]) of land. Fortuitously, Thomas' father leased his young son's tract for oil exploration during 1906–1908. The first hole was a gusher as were 41 other wells of the 49 drilled on the tract. Thomas, upon attaining age, acquired substantial wealth from his expanding petroleum enterprises in Oklahoma and Texas. While on visits to Paris to oversee his company's European business-

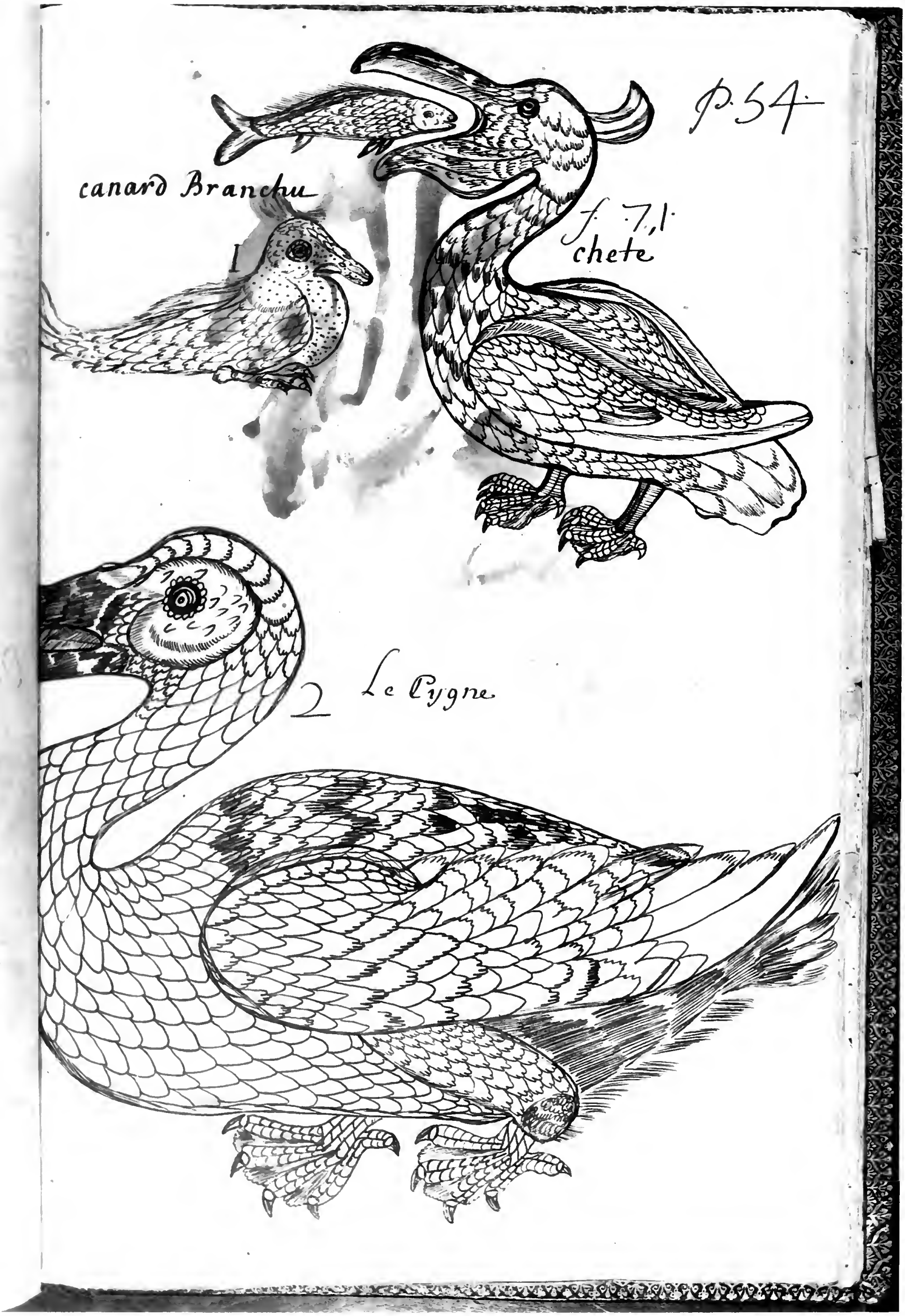

FIG. 1. Three waterfowl from Nicolas' Plate 54 with *Codex* captions, the name used by Nicolas, the current English and French common names, and the modern scientific name in parentheses. 1. Top left (Canard Branchu, Wood Duck, canard huppé, *Aix sponsa*). Top right (Chete, American White Pelican, pelican blanc, *Pelecanus erythrorhynchos*). 2. Bottom (Le Cygne, Swan, *Cygnus* spp.).

es, he developed an abiding interest in the visual arts and old literature, leading him to visit countless art museums, galleries, and auctions, and to meet with other art connoisseurs and dealers. Gilcrease began buying early manuscripts whenever he could. The *Codex* manuscript was one of his most prized acquisitions among thousands. Amazingly, Gilcrease failed to keep detailed records of his purchases and we know only that he acquired the *Codex* "after 1930," probably in 1949.

Eventually his interests drifted to artifacts of his native brethren and the treasures of renowned western artists such as Remington, Moran, and Russell. Needing a depository to safely preserve his trove and to make it available for public display and study, Gilcrease created a magnificent museum bearing his name. It opened on 2 May 1949 in Tulsa. Other than for his treasured collections, wealth did not bring him a great deal of happiness, nor did his eventually failed marriage to appropriately named Norma Des Cygne, former Miss Oklahoma and Miss America. Thomas Gilcrease died in 1962.

Most of the illustrations in the *Codex* deal with waterfowl (Anatidae), hawks and eagles (Accipitridae), upland game birds (Phasianidae), and owls (Strigidae). We selected one plate representative of Nicolas' avian illustrations. No portraits of Nicolas are known.

In Figure 1, the reasonably life-like illustration of the Chete, the pelican, correctly shows its general posture, long mandible, pouch, and its piscivorous habit. However, the Canard Branchu or the Wood Duck, while accurately named for its tree-perching behavior is quite unlife-like and could more readily pass for a columbid than an anatid. The Le Cygne, either a Trumpeter (*Cygnus buccinator*) or a Tundra Swan (*C. columbianus*), both of which might be found at that time in areas visited by Nicolas, appears unnaturally posed, too rotund, squat, and short-legged. However it does reflect the decreasing sizes of individual upper wing feathers anteriorly from the primaries through the coverts.

In considering the relative accuracy of these and others he depicted, one must consider that Nicolas was untrained either as an artist or an ornithologist, and it seems probable that he, unlike many succeeding avian illustrators, may have lacked reference specimens and field sketches. Nicolas' drawings would be even more remarkable if they had been done, in fact, in the field or simply from memory.

G. Dostie (Editor, "Codex du nord Ameriquain," 1701. Charles Becard, Sier de Grandville. Media-Teq & Parti Pris Montreal, Quebek), in praise of the *Codex* (1981:7) states, "No other work is more fundamental and inquiring in the knowledge of North American civilization. . . ." This may be overly effusive. Nevertheless, "*Codex canadiensis*" endures as an extraordinarily rich source of natural history information about New France, and establishes Nicolas in the ranks of Boucher, Denys, Lescarbot, and Marie-Victorin as early Canadian naturalists.

We look forward to the English translation of *Histoire*, a task now underway by Nancy Senior, Head, Department of Language and Linguistics, University of Saskatchewan, Saskatoon; François-Marc Gagnon, Gail and Stephen Jarislowsky Institute for Studies in Canadian Art, Concordia University, Montreal; and with the ornithological expertise of Michael Gosselin of the Canadian Museum of Nature, Ottawa. Figure 1 is reproduced with the permission of the Gilcrease Museum, Tulsa, Oklahoma, USA.—HENRY M. REEVES, 22250 Boulder Crest Lane SE, Amity, OR 97171, USA and C. STUART HOUSTON, 863 University Drive, Saskatoon, Saskatchewan, S7N OJ8, Canada.

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Ornithological Literature

Compiled by Mary Gustafson

THE WHITE-CHEEKED GEESE: *BRANTA CANADENSIS*, *B. MAXIMA*, *B.* "*LAWRENSIS*", *B. HUTCHINSII*, *B. LEUCOPAREIA*, AND *B. MINIMA*. TAXONOMY, ECOPHYSIOGRAPHIC RELATIONSHIPS, BIOGEOGRAPHY, AND EVOLUTIONARY CONSIDERATIONS. VOLUME 1. EASTERN TAXA. By Harold C. Hanson. Avvar Books, 203 South Palm Drive, Blythe, California, USA. 2006: xxiii + 420 pp., 38 maps, 39 morphometric diagrams, 13 tables, 398 photographic illustrations, 14 plates, and 6 graphs. ISBN: 0-9708504-3-3. $25.00 (soft cover), $80.00 (cloth).—The late Harold Hanson spent the greater part of his life studying White-cheeked (Canada, to most of us) Geese at the Illinois Natural History Survey. This is the first of two volumes that present the results of his work, published posthumously by Bertin W. Anderson, who put the finishing touches to the not quite completed manuscript. The work is based on the study of preserved skins and skeletons of more than 1,800 geese in the collection of the Illinois Natural History Survey (INHS), as well as hundreds examined in, or borrowed from, other museums. Hanson also observed hundreds of thousands of geese in the field, in breeding areas or on migration. Much of Hanson's work was supported by contracts from the U.S. Fish and Wildlife Service (USFWS) in the hope that a better taxonomic understanding would provide additional management tools for this important game species.

The volume includes a Foreword by Harvey K. Nelson of the USFWS, a Preface, Acknowledgments, and a critical Editors' Note. Chapter 1 is the rather short introduction to the entire work, both volumes. It includes an overview, sections on the challenges of collection and preparation of appropriate material, criteria for the recognition of species and subspecies, selection of holotypes and of names, illustrations and layout of the book, and flyways used by the geese. Two chapters are devoted to ecophysiography, and seven to descriptions and discussions of the subspecies in parts of the area covered.

In a way, this is two works in one. One is a discussion of the ecophysiography of northeastern Canada, from the Hudson and James Bay lowlands to the east coast. This is covered in two long, profusely illustrated chapters and, to some extent, in the accounts of the taxa involved. This discussion takes into account the geological history, modern topography, and vegetation of a large number of "physiographic units." I am not qualified to discuss the originality or accuracy of this material. Its importance, however, is to set the stage for the taxonomic and nomenclatural section of the volume, for which Hanson states (page 363): "the rule prevailing for the taxonomy and biogeography of White-cheeked Geese: for every race there is a corresponding unique isolated ecophysiographic unit." Equally important is the converse of that rule.

As the title of the book (the names are on the title page, but not the cover) indicates, Hanson recognizes six species in the Canada Goose complex, of which five were previously recognized as subspecies. Volume 1 contains the first 10 of at least 34 chapters and covers the portion of the range of the complex in northern Canada east of the Hudson and James Bay lowlands, roughly east of Churchill. Only parts of two species are covered. The text (page 3) states: "Although a total of 193 taxa of the White-cheeked Geese are recognized in this study (Table 1.1), possibly 10–15 remain to be found and described." Table 1.1 (pages 23–27) is a list of all the taxa to be discussed in both volumes. It actually lists 218 names, one as a species and 217 as subspecies—although one subspecific name is omitted. Of the 217 named taxa, only 35 are covered by accounts in Volume 1, leaving 182 for the proposed second volume. Two names in Volume 1 and 10 others in Volume 2 are presently recognized as available names; the rest are or will be newly described and named.

Of the 35 names of taxa covered in Volume

1, seven are deliberately used in a manner that makes them unavailable, so that only 26 new names are proposed in such a way that they are available under the International Code of Zoological Nomenclature. Hanson originally intended that 33 new subspecific taxa be described in this volume. However, Anderson recognized a problem (Editors' Note, page ix) that "involved naming a taxon on the basis of a single specimen, often taken on the wintering grounds and with no specific information about where the specimen that represents a population breeds." In an attempt to avoid formally introducing names for seven such taxa, the editors placed those names in quotation marks wherever used and deliberately did not use the term "new subspecies" or the equivalent where the names were used to introduce subspecific accounts or "racial biographies." However, there is a full description of each taxon placed in quotation marks, including the designation of a holotype. The editors have placed quotation marks around another 50 names in Table 1.1 and elsewhere in the text, that will be fully discussed in Volume 2; even there they presumably will not meet the criteria for availability.

However, several accounts for taxa with properly introduced names based on wintering birds also have no specimens from breeding areas mentioned in the text—but only localities of specimens from the INHS collection are listed. Of the 26 newly proposed taxa, only 11 have designated holotypes from the presumed breeding range of the taxon; the other 15 are named from specimens taken in migration or in wintering areas. It is thus impossible to relate most of the new names to breeding populations of this highly migratory complex, making those names useless in any future evaluation of geographic variation. For some of these races, breeding areas are somewhat arbitrarily stated to be one or another of the physiographic units discussed elsewhere. As one example (page 361): "Using the peg-and-hole analysis, a breeding grounds somewhere in the northern half of the Lowlands is plausible." The words "assumed," "presumed," and "apparently" are used for about half the statements on breeding areas of the newly described subspecies. The caption for Fig. 9.42 indicates the area shown "does not appear to be suitable for breeding geese; yet, for lack of a suitable alternative, I have tentatively assigned the breeding range of [a newly named race] to it."

In at least four instances, Hanson designated specimens from the same wintering locality as holotypes for two separate subspecies. In one instance the two birds were collected only 4 days apart; in another, they were taken in the same month. Although different breeding populations of these geese certainly overlap in wintering areas, it is highly likely in these instances that the two individuals were members of the same breeding population. The concept of individual variation within a population is virtually absent from this volume. Every slight variant might be the basis for a new name, if an unused breeding area could be carved out.

There are 14 full-page plates showing lateral and dorsal bill profiles of 89 subspecies. Accompanying each set of profiles are three numbers, unmentioned in the captions but identified elsewhere (page 80) as the length of the exposed culmen of the specimen photographed (from which photograph the drawing was traced), and the height and width of the culmen as percentages of the length. These values, based on individuals, are similar to values of these data for age-sex classes of populations given in accompanying tables and presumably typify the races. Each racial biography is accompanied by one or more morphometric diagrams. In these, spokes radiating like a clock face represent 12 measured characters; mean values (from the center) are joined by dotted lines to form rough circles or ovals to define the subspecies. These are accompanied by tables presenting the same data. Many such diagrams, perhaps 40%, are based on only one or two specimens of an age-sex class. For at least a few of the subspecies, these diagrams if scanned and overlapped (as done for me by Christina Gebhard and Brian Schmidt) are essentially identical, indicating they are not particularly useful in characterizing or identifying subspecies.

This seems to be a work that was in progress almost until the moment of the author's death. In fact, the many inconsistencies, too many to be detailed here, suggest that it was a work that was constantly being modified and added to, often without revision of previous writing to recognize the additions or changes. For example, the winter range of one newly named race is thought to be around Chesapeake Bay in the racial biography. However, a few pages later that race is said to follow "markedly bifurcate [migration] routes that terminate in wintering grounds lying 700 miles apart."

Accounts for some subspecies were inserted when the races were recognized, well after many of the accounts had been completed. The caption for Map 9.7 gives place names delimiting ranges of subspecies, but many names are not on the map. It refers to "gazetteer map 4.1" for localities but Map 4.1 is of Anticosti Island, not relative to this section. Map 5.1 may have been intended, although not all the names are there, either. This suggests that chapters were renumbered at some stage, or perhaps one was inserted. Most of the maps do not have coordinates or scales. Many fade out toward the edges from poor drawing or poor printing.

To what extent will this book, and the anticipated similar companion volume naming an additional 200+ subspecies on the rest of the continent, serve as a tool for management and conservation? Very slight, if any, in my opinion. Will it help museum curators identify and arrange their collections? I doubt that any will try. Does it relate geographic variation to ecophysiography? Not beyond stating a 1:1 relationship between areas and races. Will it serve as a model for future taxonomic research? I hope not. Should you have this book on your shelf or in your library? Only if you really love geese or northeastern Canada.

Positive things about this work include the large number (~300) of habitat photos, mostly aerial, of northern wilderness that most of us will never see. These might be more useful if dated. Many of the taxa named (or to be named) honor early explorers or naturalists of the northern lands, giving interesting historical tidbits.—RICHARD C. BANKS, Department of Vertebrate Zoology, National Museum of Natural History, MRC 111, P. O. Box 37012, Washington, D.C., USA; e-mail: banksr@si.edu

HANDBOOK OF AUSTRALIAN, NEW ZEALAND, & ANTARCTIC BIRDS (HANZAB). VOLUME 7. BOATBILLS TO STARLINGS. Part A: Boatbills to Larks; Part B: Dunnock to Starlings. Edited by P. J. Higgins, J. M. Peter, and S. J. Cowling. Oxford University Press, Melbourne, Australia. 2006: 1,984 pp., 54 color plates, numerous range maps, line drawings, and sonograms. ISBN: 0-195-53996-6 (set of A & B). $424.50 (cloth).—This, the final volume in this mammoth series, completes coverage of the Order Passeriformes. It proved to be too long to publish as a single book and, hence, consists of two separately bound parts. Twelve families are covered in Part A (pages 1–1056), Dicruridae (fantails, drongos, monarch flycatchers, and boatbills) to Aludidae (larks) and includes 75 species. Sixteen families are covered in Part B (pages 1056–1984), Prunellidae (accentors) to Sturnidae (starlings and mynas) and includes 94 species. The species accounts vary in length from less than one page for the Willow Warbler (*Phylloscopus trochilus*), an unconfirmed vagrant in the HANZAB region, to 50 pages for the Australian Magpie (*Gymnorhina tibicen*), a widespread polytypic species.

The species accounts for each family are preceded by a family account, usually of 3–4 text pages, including the references cited. Species accounts begin with the scientific and common names, other English names, and a listing of subspecies for polytypic forms. Typically then follow sections on field identification, habitat, distribution and population, threats and human interactions, movements (including a section on banding data and longevity), food (including foraging behavior), social organization, social behavior, voice (including sonograms), breeding, plumages, bare parts, molts, measurements, weights, structure, age and gender identification, and geographical variation (including detailed treatment of subspecies). The account concludes with a references section. Taxonomy generally follows Christidis and Boles (1994, RAOU Monograph 2, Melbourne), augmented by Schodde and Mason (1999, CSIRO, Melbourne). Range maps depict areas of documented breeding in red and areas of occurrence in half-tone red. Red arrows point to island occurrence.

The color plates by P. R. Marsack, N. Day, K. Franklin, P. J. Slater, J. Luck, and D. J. Onley are uniformly excellent, and depict multiple images to show differences by gender, age, and subspecies plumages where appropriate. For example, for the polytypic Singing Bushlark (*Mirafra javanica*), 16 images occupy the entire plate. Many plates show birds in flight. For example, one plate illustrates three currawong species (Artamidae) perched and a subsequent plate shows them in flight. Line drawings supplement a few species accounts.

Volume 7 completes this handbook series. The project started in 1981 with Royal Australasian Ornithologists' Union (RAOU) (now Birds Australia) Council approval for production of a four-volume coverage of the birds of Australia, patterned after the *Handbook of the Birds of Europe, the Middle East, and North Africa.* By 1985 Antarctica and New Zealand had been incorporated into the project and by 1989 a contract had been signed with Oxford University Press to publish the series. Volume 1 was published in two parts (volumes) in 1990 and $A8,000,000, 957 species, and 26 years later the project has been completed. In a section "Finishing HANZAB—A Reflection," Peter Higgins, a senior editor throughout the project, summed up the purpose of the project, "From the outset, the major goals of the project have been, firstly, to summarize all that we know of the birds of Australia, and later New Zealand and the Antarctic, and to make clear what we do not know; and, secondly, to prepare detailed summaries of the plumages and other external morphology of all species, describing and analyzing all sources of variation observed." In all these they have admirably succeeded. Because the 'what we do not know' is so striking, the heuristic value of the series should be immense. For example, in the species account for the Yellow-breasted Boatbill (*Machaerirhynchus flaviventer*), we find: "MOVEMENTS Little known," "[foraging] **behaviour** Poorly known . . . ," "SOCIAL ORGANIZATION Very poorly known," "SOCIAL BEHAVIOUR Very poorly known," "VOICE Not well known," "BREEDING Poorly known. . . . " There are comparatively few ornithologists in Australia and the opportunities for research are, as a result, extensive.

Volume 7, as with earlier volumes, is well organized, thoroughly researched, well illustrated and exhaustive. The range maps are detailed and easy to read. I particularly like that the references for each family or species account are listed at the end of the account rather than at the end of the volume, but I have always been irritated by the abbreviation of citations—the titles are not included. This series is the first place I turn to for information on Australasian birds. It is simply indispensable for anyone with a serious interest in birds of this region. The volumes are expensive, so academic and larger public libraries should be encouraged to acquire the series. The RAOU (Birds Australia) is to be congratulated on producing such an important series of books.—WILLIAM E. DAVIS JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, MA 02536, USA; e-mail: wedavis@bu.edu

BIRDS OF SOUTH AMERICA—NON-PASSERINES: RHEAS TO WOODPECKERS. By Francisco Erize, Jorge R. Rodriguez Mata, and Maurice Rumboll. Princeton University Press, Princeton, New Jersey and Oxford, United Kingdom. 2006: 384 pages and 158 color plates. ISBN: 0-691-12688-7. $29.95 (paper).—We have waited a long time for the first English language field guide to treat all non-passerine species of birds of South America. It fills a huge and important niche for field ornithology in the most species rich of continents. For the first time, we no longer have to just imagine all South American hummingbirds, hawks, tinamous, puffbirds, etc. in one handy volume. It's hard to overstate the size of this enormous task (the Introduction explains the book had its start in 1970) and how badly it has been needed. The book is billed as an "illustrated checklist," perhaps an attempt to distance itself from the field guides that have tended more towards comprehensive handbooks best left at home. At a compact 127 × 177 mm (5 × 7 in.) and scarcely 25 mm (1 in.) thick, this book is truly a field guide for bird identification and is much more than a checklist (to me "checklist" implies little more than a stapled list of bird species and, even if illustrated, not with such high quality plates and accompanying text).

The book opens with the usual acknowledgments, preface, two introductions (one titled "the birds in this book"), and an essay on conservation, the last of which is placed a bit awkwardly after a list of abbreviations and a map of the continent, and before the usual page showing external anatomy used in describing field marks. Following these is a unique and interesting, but perhaps not so useful chapter introducing each family. Each family receives two to nine paragraphs describing various characteristics including those of behavior, habitat, and breeding, as well as a summary of worldwide distribution and diversity. The latter part of the account for Odontophoridae seems to have been inadvertently deleted mid-sentence. The next 333 pages (87% of the book) comprise the species accounts and plates. The illustrations are opposite the accounts, each of which is also accompanied by a small range map. Finally, there is a concise glossary, a section on further reading, and (thankfully) a single index, with both English and scientific names together. A quick check of several pages indicated the indexing was well executed.

In general, the illustrations are wonderful, the maps only okay, and the text and execution of the design sloppy. I'll first attend to the criticisms.

After already noticing several typos in the first sections (including a name in the acknowledgments) I discovered my major disappointment with the book in the explanation of the taxonomic treatment. After reading, "In the lack of any official check-list of the birds of South America . . . " I had to pause and check the publication date to be sure I wasn't given a decade-old proof. It's hard to believe this is merely a mistaken assumption of the authors. How could they not be aware of the list created by the South American Classification Committee (SACC), sanctioned by the American Ornithologists' Union since 1999 and available to anyone with an Internet connection for nearly 6 years by the time this book went to press (Remsen Jr., J. V. et al., Version 2006, http://www.museum.lsu.edu/~Remsen/SACCBaseline.html)? Cited in technical literature, including peer-reviewed interdisciplinary journals, the result can certainly qualify as an official checklist. The authors admit the existence of a newer taxonomy offered by the *Handbook of Birds of the World* (del Hoyo, J. et al. Volumes 1–7, 1992 to 2004, Lynx Edicions, Barcelona, Spain), but that too is admittedly ignored in many cases. Their main excuse seems to be the opinion that recent splits are only a result of the "publish or perish" pressures in academia and will soon be re-lumped anyway. This shows a complete lack of understanding of current taxonomic research and how a committee such as the SACC operates, where proposals can be submitted by anyone and where the committee members are volunteers who evaluate published evidence independently without any pressure from their respective institutions (and not all work for academic institutions). Complaints regarding "taxonomy by committee" do not apply here and there isn't a good reason not to have followed SACC taxonomy. By not doing so this book suffers. Not only are there over 50 species missing from the book (the SACC list includes 1,352 non-passerines as of December 2006), but even recent understandings in higher level taxonomy are ignored, such as conjoining the Anseriformes and Galliformes (they are instead separated by unrelated orders). The resulting "taxonomy by author" approach has also resulted in some unique names, combinations, and omissions not conducive to communication. A few examples include: "Orange-headed Vulturine-parrot" rather than "Bald Parrot" for *Pionopsitta aurantiocephala* (a Google search for the former doesn't yield any hits; the latter gets 1,720); *Otus koepckeae* is mentioned as a race of *O. choliba* (also zero Google hits); the distinctive "Cliff Parakeet" (*Myiopsitta monachus luchsi*) isn't mentioned at all. In a few cases, this treatment result in splits not accepted by the SACC such as Loja Hummingbird (*Amazilia alticola*; mentioning that it is probably a race of *A. castaneiventris* was an error, as was referring *A. rondoniae* as a probable race of *A. francia* on the same plate).

An attempt to include additional subspecies or races (indicated by an "R" next to the illustrations) was perhaps a good idea, but was executed so poorly as to negate any benefit. While the species accounts sometimes describe these additional subspecies, it is not indicated to which of the additional illustrated forms the "R" is being referred. At times, they aren't even named and only rarely is distributional information given. One might assume the species description and the form illustrated without the "R" is the nominate form, but this is far from clear. The account for Versicolored Emerald (*Amazilia versicolor*) demonstrates the confusion created; after the species description, two additional subspecies are described, but the plate shows four forms, three with an "R." Comparing the text with the pictures, the description of the presumed nominate form matches one of the illustrations that received an "R." The list of abbreviations on page x includes an "R[1]" for additional races, but I couldn't find this used anywhere, not that it would have helped. Actual notes on the plates, such as those used for the Rufous-thighed Hawk (*Accipiter erythronemius*) complex would have been helpful. Uniquely and inexplicably in the case of Pfrimer's Parakeet (*Pyrrhura leucotis pfrimeri*), an asterisk rather than an "R," is used.

Further gripes: On several plates, the numbering begins in the upper right rather than the upper left and then proceeds in a nearly random order, making awkward the task of matching the species accounts. This has resulted in the authors' own confusion, where species numbers are mis-referenced (i.e., the Loja Hummingbird example and the same error on the same plate in the account for Blue-green Emerald [*A. rondoniae*]) or where species' numbers are missing (male Peacock Coquette [*Lophornis pavoninus*] and Purple-throated Woodstar [*Calliphlox mitchellii*]). The voice description of Long-tailed Potoo (*Nyctibius aethereus*) is missing the distinctive series of owl-like hoots. The rump color of the Black-hooded Sunbeam (*Aglaeactis pamela*) is described as emerald rather than turquoise blue (and the tiny bit of rump illustrated looks green). The account for Red-fronted Macaw (*Ara rubrogenys*) doesn't mention agricultural fields as a habitat and the immature plumages of flamingos are missing. I didn't read the entire field guide and lack experience with a vast majority of the species, so these are clearly only a few examples.

The range maps are fairly accurate and serve their purpose, but those who expect the wealth of biogeographical detail that can be easily portrayed in such maps will be disappointed. They are small scale and give only an imprecise idea of distributions on a continental scale; the simple task of zooming in on highly limited ranges was not undertaken. The colors used in the range maps are inconsistent, different enough even on the same page to suggest that additional information was meant to be portrayed (such as relative abundance). I could not find an explanation and assume it is merely a result of different generations of map making. This should have been explained.

So far, my criticisms have honed in on the failings of the book's text, plan, and execution. Obviously, the illustrations are the part of the book first examined, most quickly critiqued, and most often used. I have almost no complaints and much praise for this section of the book. The artwork is beautiful, accurate, abundant, and a pleasure to view. One minor complaint might be that the archaic (and arguably sexist) practice of illustrating females only partially, reduced, and/or behind the males (such as among the hummingbirds) should have been avoided (in some plates females *are* pictured in the foreground, but the males are not reduced). The little vignettes amidst the main illustrations are nice, showing interesting and perhaps useful behaviors and postures, but it is not always clear what they are trying to show. An example is the crouched, tail-raised posture shown for Great (*Tinamus major*) and Tataupa (*Crypturellus tataupa*) tinamous. I have not seen this behavior, but it must be sufficiently interesting to warrant the extra illustrations. I read both species accounts and the family description without finding an explanation. Other vignettes are confusing, such as the juvenile Tiny Hawk (*Accipiter superciliosus*) not only being larger than the adult but also the same size as the Gray-bellied Goshawk (*A. poliogaster*) in flight next to it.

A book of this scope will be thoroughly scrutinized and more criticisms are sure to be found as it is too huge of a task to execute perfectly. It is a tremendous accomplishment and an excellent product (not to mention easy on the luggage load). I think every neotropical field ornithologist and birder will want to own one.—RICHARD C. HOYER, WINGS, Inc., Tucson, AZ, USA; e-mail: calliope@theriver.com

ECOLOGICAL CONSEQUENCES OF ARTIFICIAL NIGHT LIGHTING. Edited by Catherine Rich and Travis Longcore. Island Press, Washington, D.C. 2006: 458 pp., 15 black and white photographs, 24 illustrated drawings, 26 graphs, and 21 tables. ISBN: 1-55963-128-7. $65.00 (cloth). ISBN: 1-55963-129-5. $29.95 (paper).—A recurring refrain throughout the book is what is not known and what needs detailed investigation, and in most cases fundamental data, on how artificial light is affecting life at night. From the editors' work with geography, the environment, and conservation, this work was born first from their discovery about how little we know about the effects of existing and growing amounts of artificial night lights, which in turn stimulated them to convene an international conference addressing the topic in 2002 from which most of the chapters in this work were drawn. The book's principle purpose is to describe how night lighting generated by humans influences global ecosystems by considering how it affects or potentially affects select taxa that evolved under patterns of natural light and dark.

After an introduction (Chapter 1) that describes an overview of the topic, the taxa considered are mammals (Chapter 2, terrestrial species by Paul Beier; Chapter 3, bats by Jens Rydell), birds (Chapter 4, select migratory species by Sidney A. Gauthreaux Jr. and Carroll G. Belser; Chapter 5, select marine birds by William A. Montevecchi; Chapter 6, Black-tailed Godwit by Johannes G. de Molenaar, Maria E. Sanders, and Dick A. Jonkers), reptiles and amphibians (Chapter 7, sea turtles by Michael Salmon; Chapter 8, reptiles in general by Gad Perry and Robert N. Fisher; Chapter 9, frogs and toads by Bryant W. Buchanan; Chapter 10, salamanders by Sharon E. Wise and Bryant W. Buchanan), fishes (Chapter 11 by Barbara Nightingale, Travis Longcore, and Charles A. Simenstad), invertebrates (Chapter 12, insects attracted to street lamps by Gerhard Eisenbeis; Chapter 13, moths by Kenneth D. Frank; Chapter 14, fireflies by James E. Lloyd; Chapter 15, select freshwater species by Marianne V. Moore, Susan J. Kohler, and Melani S. Cheers), and plants (Chapter 16 by Winslow R. Briggs). Each treatment attempts to provide an overview of the effects of artificial night lighting; wherever appropriate the authors offer recommendations to eliminate or mitigate known or suspected negative influences. The book concludes (Chapter 17) with a synthesis by the editors in which they use biological levels of organization to address how artificial night lighting does or could affect physiology, behavior and populations, communities, and ecosystems.

In addition to the three chapters devoted specifically to birds, the effects of avian predators acting under artificial night lighting are noted throughout the work (e.g., among others, Chapter 11, fishes; Chapter 12, insects; Chapter 13, moths). Gauthreaux and Belser (Chapter 4) briefly review the literature on the attraction of birds to night lighting, to include a select treatment of avian vision, sources of attracting lights (lighthouses, light ships, floodlights and ceilometers, city lights and horizon glows, fires and flares, and broadcast and other communication towers). For tall communication towers, they provide more detail, presenting unpublished results on the influence of lighting type and the behavior of night migrants near tall communication towers in South Carolina. We learn that controlling the extent to which night lighting is directed upward and outward (from buildings, billboards, street lights, tower warning lights), especially during migratory periods and when cloud ceilings and visibility are low, will reduce the risk of attracting birds to these hazards where they can be killed striking guide wires or the metal, concrete and glass from which they are constructed. Although more studies are ongoing and required for a complete understanding, current evidence suggests that white (possibly red) strobe lighting may attract fewer migrants to tall structures than continuous lighting. Turning off night lights in multistory buildings wherever they occur can reduce migrant mortality and offer energy and its associated cost savings. The authors highlight measures adopted by the City of Toronto, Ontario at the urging of the Fatal Light Awareness Program (FLAP; www.flap.org) to lessen the attraction of this urban center by various measures to make buildings and their lighting less of a threat to night migrants; following the lead of Toronto, similar programs are currently underway or developing in Chicago (IL), Detroit (MI), Milwaukee (WI), Minneapolis-St. Paul (MN), New York (NY), and Philadelphia (PA). Meager published evidence document birds being killed outright by striking the opaque walls of upper story lighted buildings, but a large and growing data base describes how night lighting atop buildings, especially during inclement weather with low cloud cover, draws migrants in and, as if captured by the light, they fly erratically in and out of the beams and glow, seemingly confused, physically stretched to exhaustion, some escaping from predators (DeCandido and Allen. 2006. Wilson J. Ornith. 118: 53–58) and then dropping or fluttering to the ground for rest and safety to await the first hint of natural light. Once on the ground, now within urban canyons they are killed in currently uncountable numbers striking glass panes of all sizes or killed outright by predators or taken by scavengers (among others: crows, gulls, cats, rats, squirrels, even chipmunks and humans). Montevecchi (Chapter 5) reviews the principal sources of artificial light in the marine environment and its effect on seabirds. We learn that lighthouses, near- and offshore fisheries that use intense lighting to attract their intended catch, and offshore oil and gas platforms with their open flame flares are sources of avian mortality that could be substantial but are currently not systematically monitored or studied effectively. Among those particularly at risk are species of special concern, fledglings on their initial flight to sea, and adult migrating flocks. Investigating how roadway lighting affects the breeding ecology of Black-tailed Godwit (*Limosa limosa*) in a wet grassland in The Netherlands, de Molenaar, Sanders, and Jonkers (Chapter 6) inform us, after caution about the preliminary nature of their study, that: (1) road lighting has a small but statistically significant negative effect on breeding, influencing an area 300 m or 60 ha/km from a lighted road, (2) road lighting seems to have a small negative effect on the timing of the breeding period, and (3) no conclusive evidence was obtained to demonstrate an association between road lighting and egg predation.

There are no substantive criticisms in the production or content of this work. The specific and special treatment the editors and authors give to this topic is long overdue. We learn, primarily from Moore, Kohler, and Cheers (Chapter 15), that as essential as how to measure artificial night lighting is in need of standardization, there is also the need for more sophisticated instrumentation to do it. With the possible exception of sea turtles beginning in the 1960s (McFarlane 1963, Copeia 1963:153), studies are needed to investigate the effects of artificial night lighting on other taxa at the molecular to ecosystem levels of organization. Surely, artificial night lighting has illuminated the planet long enough to have influenced the evolution of several taxa, especially those with short generation times, and yet this type of lighting is but a flicker in the history of the Earth such that its potential to cause harm to those which have evolved under natural light and dark cycles seems obvious if not self-evident. This book helps immeasurably in encouraging a needed broad based series of inquiries and, more specifically, to encourage the gathering of fundamental data at all levels, especially the use of structured experimental designs to address specific hypotheses. *Ecological Consequences of Artificial Night Lighting* should be a priority acquisition for general and research libraries, and an essential read for educators, ecologists, ornithologists, and all others having interest or plans to investigate any aspect of life living with light.—DANIEL KLEM JR., Muhlenberg College, Allentown, PA, USA; e-mail: klem@muhlenberg.edu

THE WILSON JOURNAL OF ORNITHOLOGY

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Continued from outside back cover

SHORT COMMUNICATIONS

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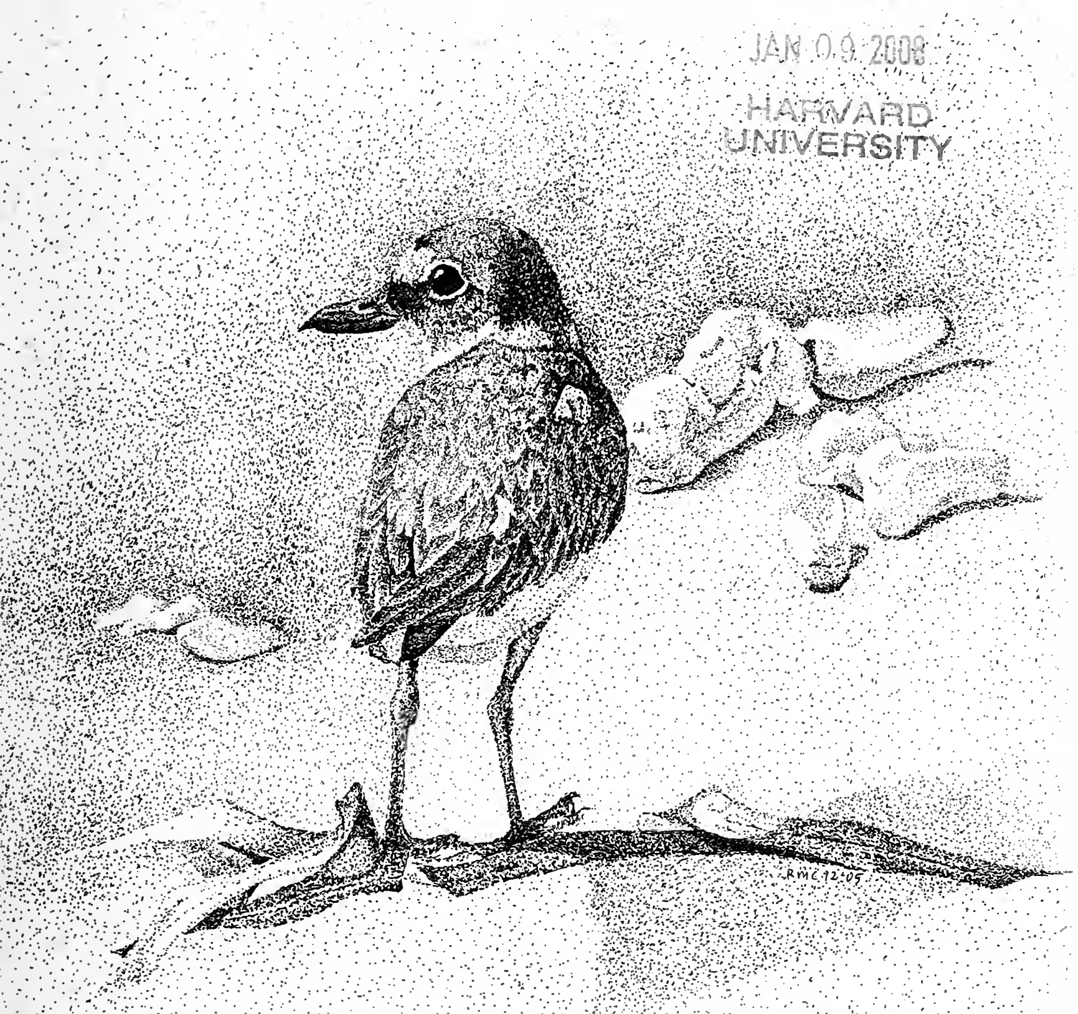
Volume 119, Number 3 CONTENTS September 2007

MAJOR ARTICLES

Continued on inside back cover

The Wilson Journal of Ornithology

Volume 119, Number 4, December 2007



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COVER: Wilson's Plover (*Charadrius wilsonia*). Illustration by Robin Corcoran.

FRONTISPIECE. The Golden-winged Warbler (*Vermivora chrysoptera*) has experienced population declines in portions of its range. A study in Wisconsin (page 523) found that abundance of Golden-winged Warblers was greatest in stands with high stem densities, particularly in young aspen (*Populus* spp.) stands. This suggests that management in the Great Lakes Region designed to create suitable habitat for this warbler could focus on maintaining shrub-scrub habitats through regeneration of aspen forests that provide quality habitat for 6–8 years. Maintaining shrub swamp habitats that support lower, but stable densities of Golden-winged Warblers over longer periods of time may also be important for the long-term persistence of this species. Photograph by Dennis E. Maleug.

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GOLDEN-WINGED WARBLER HABITAT USE AND ABUNDANCE IN NORTHERN WISCONSIN

KARL J. MARTIN,[1,3] R. SCOTT LUTZ,[2] AND MIKE WORLAND[1]

ABSTRACT.—Golden-winged Warblers (*Vermivora chrysoptera*) are declining in the eastern portion of their range partially due to a loss of shrub-scrub and early successional habitat. We surveyed Golden-winged Warbler abundance in shrub swamp, young aspen (*Populus* spp.), heavily thinned hardwood, jack pine (*Pinus banksiana*), and two edge cover types (i.e., swamp/aspen and swamp/mature) in 2002–2004 in northern Wisconsin. Golden-winged Warbler abundance was greatest in young aspen stands (1–10 years of age) and least in the swamp/mature edge cover type. Abundance did not differ among years in any of the cover types. Aspen stem density was positively related to Golden-winged Warbler abundance among stands. The presence of Golden-winged Warblers within stands, at the sampling station scale, was positively correlated with aspen stem density, the amount of low woody cover, and ground vegetation. The most effective way to manage for this species in the north central portion of its range may be through the creation of young aspen forests and by maintaining shrub-scrub habitat. *Received 7 August 2006. Accepted 31 January 2007.*

Golden-winged Warblers (*Vermivora chrysoptera*) winter in Central and South America and migrate to the Midwest, Northeast, and Appalachian regions of the United States (Confer 1992). Populations of Golden-winged Warblers have declined across their range; annual rates of decline averaged 2.4% throughout its breeding range and 2.1% in Wisconsin (Sauer et al. 2004). This decline is believed to be primarily the result of habitat loss (Smith et al. 1993, Confer and Larkin 1998) and the anthropogenic alteration of natural disturbance patterns such as fire that historically resulted in periodic creation of early successional and shrub-scrub cover types (Hunter et al. 2001). Partners in Flight ranked the Golden-winged Warbler as one of the top conservation priorities throughout their range (Rich et al. 2004) and the U.S. Department of Interior (2002) listed the Golden-winged Warbler on its list of highest conservation priority species.

Golden-winged Warblers occur almost exclusively in early seral or shrub-scrub habitat with young, dense, shrubby vegetation <3 m in height throughout their range (Hunter et al.

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2001). Recent research in aspen (*Populus* spp.) forests of north central Wisconsin reported densities of 0.49 males/ha in 1–4 year-old aspen stands; some of the highest densities recorded (Roth and Lutz 2004). These authors also reported significantly lower densities of displaying males in 6–25 year-old aspen stands. Samuel (1997) reported Golden-winged Warblers to be associated with brushy areas and particularly young regenerating aspen. Huffman (1997), reported shrub cover was higher in areas where Golden-winged Warblers were present in north central Minnesota. Golden-winged Warblers have also been found in alder (*Alnus* spp.) thickets, forest cutovers, tamarack (*Larix laricina*) bogs, and utility right-of-ways (Roth 2001, Confer and Pascoe 2003). Partners in Flight (Ruth 2004) estimated these habitat types contained 70% of the breeding population of Golden-winged Warblers in the Midwest.

Most previous research on Golden-winged Warblers occurred in the northeastern portion of their range where they were often associated with brushy old-field habitats and old mine sites. Golden-winged Warbler clutch sizes in north central New York were positively correlated with herb and shrub cover (Confer et al. 2003) with significantly greater levels of herbaceous cover in Golden-winged Warbler territories than in Blue-winged Warbler (*Vermivora pinus*) territories. Confer et al. (2003) also reported reduced numbers of Golden-winged Warbler fledglings were correlated with increased tree cover (trees >3.3 m in height). Klaus and Buehler (2001) reported Golden-winged Warblers in the Nantahala National Forest in North Carolina and the Cherokee National Forest in Tennessee occupied young stands with low basal areas and preferentially selected nest sites with high levels of herbaceous cover.

There is little information on Golden-winged Warbler abundance in other early seral cover types such as regenerating pine and hardwoods stands or in shrub-scrub communities with high levels of brush cover that resemble early seral forests such as lowland alders, tamarack bogs, and brushy swamp edges. Biologists have suggested that Golden-winged Warblers should be abundant in a variety of early seral habitats or shrub-scrub habitats that produce similar habitat conditions (Hunter et al. 2001).

We measured Golden-winged Warbler abundance between early seral habitats that resulted from management actions (e.g., regenerating aspen, hardwoods, and pines) and shrub-scrub habitats (lowland alders, tamarack bogs, and brushy swamp edges) that were independent of land management. The specific objectives of our study were to: (1) quantify abundance of singing male Golden-winged Warblers in six different cover types, and (2) assess correlations between male Golden-winged Warblers and vegetative characteristics.

METHODS

Study Area and Sampling Design.—Our study area was 8,000 km^2 in northcentral Wisconsin (Fig. 1) and represented the approximate geographic center of the Golden-winged Warbler summer range. This area is in the Superior Mixed Forest Ecoregion (Bailey 1998) and is dominated by mixed coniferous-deciduous trees and shrubs, hardwoods, and softwoods (Wisconsin Department of Natural Resources 1998). The area receives ~80 cm of precipitation throughout the year with extreme temperatures ranging from −34° C in winter to 32° C in summer. Forest management and tourism are important in the region because of abundant forests and lakes (~13% of the area is open water).

We obtained forest compartment maps and/or Geographic Information System (GIS) coverages for the study area from the Wisconsin Department of Natural Resources, USDA Forest Service, and several private landowners. We selected 42 stands for surveying with each survey stand >32 ha to minimize the influence of habitat edges. We chose edges between two adjacent stands that were at least 1.4 km in length to accommodate 7–10 point count stations. We partitioned the study area into NE, NW, SE, and SW quadrants and selected approximately the same number of stands for a given cover type in each quadrant (Fig. 1). We randomly selected stands when there were more stands than needed within a quadrant. Contiguous, accessible stands with sufficient area for 7–10 point counts were often uncommon. In these cases we selected all

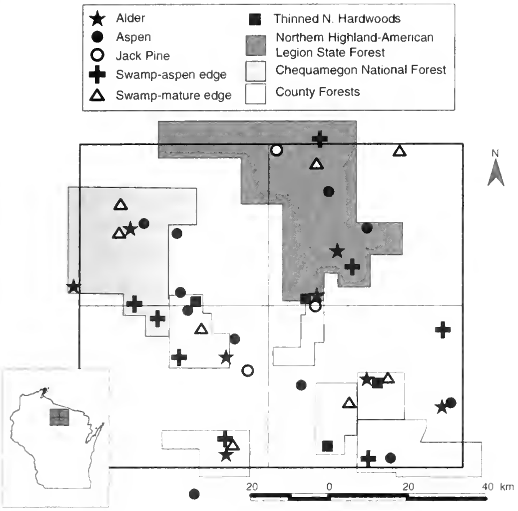

FIG. 1. Golden-winged Warbler survey area with quadrants, cover types, and public forest ownerships in north central Wisconsin.

stands available for a cover type. Stands with recent harvesting activity and average regeneration heights ≤0.70 m were not selected because they were unlikely to contain Golden-winged Warblers.

We surveyed 8 shrub swamp sites, 8 swamp/aspen edge sites, 11 young aspen sites (clearcut and regenerated using coppice methods within 1–10 years of age), 3 young jack pine sites (3–10 years of age), 4 thinned (within 10 years) northern hardwoods sites, and 8 swamp/mature forest edge sites. The jack pine and thinned northern hardwood cover types (thinned sufficiently heavily to produce potentially suitable habitat) were limited and we used all available stands within the study area. Swamp/aspen edge sites represented the ecotone between swamps and upland aspen of varying ages. Swamp/mature edge sites were ecotones between swamps and mature mixed coniferous-deciduous cover types. The shrub swamp habitat was dominated by alder, whereas the swamp habitat in the edge cover types was dominated by alder or swamp conifers including black spruce (*Picea mariana*) and tamarack. The shrub swamp and swamp habitats were unmanaged stands whereas the aspen, jack pine, hardwoods, and mature forest stands had varying intensities of past forest management from clearcutting to selective harvesting.

Data Collection.—We surveyed Golden-winged Warblers at 7–10 point count stations in each stand. Stations were ≥200 m apart and ≥100 m from stand edges with the exception of our edge sites where stations were along the edge of the two cover types. We began surveys at approximately sunrise and continued until the survey was completed, the time reached 1000 hrs CST, or weather conditions reduced bird singing or singing became hard to hear. The first 5 min at each station were spent listening and looking for male Golden-winged Warblers. We then played a tape with Golden-winged and Blue-winged warbler songs for 3 min to elicit a territorial response by either species. We played the tape at a volume that was inaudible to humans beyond 80 m in open habitat types to prevent attracting birds from adjacent survey stations. We listened for 2 min for additional birds after playing the tape. We recorded and mapped male Golden-winged Warblers heard or observed within 100 m. We avoided double counting birds by comparing maps of singing males heard at adjacent sampling stations. When there was a possibility of songs from two locations being the same bird, we recorded these instances as one bird. Our survey methods were designed to avoid double counting the same bird while maximizing detection rates by using playback tapes. Bias due to variable detection rate was low because cover types had similar vegetation structure and observers were rotated among stands.

Observers visited each site twice during 25 May–21 June 2002, 27 May–23 June 2003, and 28 May–1 July 2004. We used the greatest number of Golden-winged Warblers observed during the two annual visits to each stand as the estimate of the number of singing males per station. We used the greatest count rather than the mean because: (1) we assumed that on the visit with the lowest number of Golden-winged Warblers we missed breeding males because of inactivity or poor surveying conditions; (2) the risk of counting migrating birds as residents was low given the relatively late starting date of our surveys (91% of surveys were in Jun); (3) we emphasized avoiding double-counting males; (4) in our experience, Golden-winged Warbler singing is highly variable during a short singing period; and (5) Toms et al. (2006) concluded that using the maximum number of singing males at point counts was a more sensitive index to abundance than mean values.

We collected data on vegetation structure in July or August of the first year a stand was surveyed. We centered a 12.6-m radius plot (0.05 ha) at each point count station and recorded all trees >10 cm diameter breast height (dbh). We used 1-m^2 plots at 6 and 12 m distances from the center point in each cardinal direction and recorded the number of trees <10 cm dbh for aspen and alder. We combined all remaining tree species into one group referred to as 'all other trees'. We visually estimated percent woody cover below breast height, percent bare ground, and percent tall forb cover in each 1-m^2 plot. We recorded the percent of low forb cover and percent grass cover by moving aside the shrubs and tall forbs and carefully observing the vegetation at ground level.

Data Analysis.—We standardized data across stands with differing numbers of sampling stations by using the average number of Golden-winged Warbler males per survey station across years as our response variable. We compared Golden-winged Warbler abundance across the six different cover types with analysis of variance (ANOVA). We used multiple comparisons (Tukey's Studentized Range, *alpha* = 0.10) (SAS Institute 2003) to examine if abundance varied between individual cover types.

We summed low forb cover and grass that resulted in a new measure referred to as 'ground vegetation'. Understory vegetative variables (% low woody cover, % tall forb cover, % bare ground, % ground vegetation) collected were used in a correlation analysis to reduce the number of understory variables. We considered a correlation coefficient ≥0.60 between variables significant and used this to reduce the number of understory variables to % low woody cover and % ground vegetation.

We used five vegetative variables (aspen, alder, all other trees, ground vegetation, low woody cover) and conducted a literature review to generate a subset of 15 habitat models to assess Golden-winged Warbler habitat selection across all cover types. Golden-winged Warblers have been closely associated with aspen and alder cover types so we generated habitat models by combining either alder or aspen with the understory measurements. We used multiple linear regression models for the stand scale analysis where our response variable was males/station and the explanatory variables were vegetation variables averaged across stations. We used Akaike Information Criterion (AIC) (SAS Institute 2003) values to identify which models best explained variation in Golden-winged Warbler densities across stands. AIC_c was used instead of AIC for all model building to account for relatively small sample sizes (Burnham and Anderson 2002:66–80). We assessed the relative importance of individual habitat variables by summing AIC_c weights for individual variables across all models (Burnham and Anderson 2002). Explanatory variables with relatively high AIC_c weights are considered most important for explaining the relationship between the response and explanatory variable.

We also used AIC to rank linear regression models of habitat associations at the sampling station scale. A binary response variable reflected whether a station was used or not used. A station was considered 'unused' and assigned a value of '0' as the response variable if the mean number of birds detected per survey over all years was <0.50. A station was considered 'used' and assigned a response variable of '1' if the overall mean number of birds detected over all years was ≥0.50. We used the same vegetative variables from the stand scale analysis to develop 15 habitat models to assess Golden-winged Warbler habitat selection within stands. Akaike Information Criterion (SAS Institute 2003) values were used to identify which models best explained the variation in Golden-winged Warbler use at individual sampling stations. We assessed the relative importance of individual habitat variables by summing AIC weights for individual variables across all models (Burnham and Anderson 2002). Explanatory variables with relatively high summed AIC weights were considered most important for explaining the relationship between the response and explanatory variable.

RESULTS

Stand Scale.—We recorded 142 Golden-winged Warblers across 28 stands in 2002, 177 across 42 stands in 2003, and 157 across 42 stands in 2004 with an average of 4.25 birds/stand/year (range = 0–15). We did not

TABLE 1. Golden-winged Warblers (males/station)[a] by cover type and year.

Cover type (stands[b]/stations[c])	2002	2003	2004	Overall
Shrub swamp (8/71)	0.31	0.35	0.22	0.29
Aspen (11/113)	0.79	0.71	0.68	0.75
Jack pine (3/29)	0.27	0.43	0.50	0.40
Thinned northern hardwoods (4/37)	0.27	0.11	0.14	0.17
Swamp – aspen edge (8/76)	0.57	0.43	0.36	0.41
Swamp – mature edge (8/70)	0.05	0.10	0.03	0.07
ANOVA *P*	0.071	0.044	0.004	0.001
Annual, overall (42/396)	0.44	0.41	0.35	0.41

[a] Abundance estimates are the maximum number of males detected on two sampling occasions per number of stations.

[b] Number of stands surveyed for a given cover type. Each stand was at least 32 ha or, for the edge cover types, at least 1.4 km in length.

[c] Number of stations surveyed across all stands of a given cover type. Each stand was sampled with 7–10 stations separated by 200 m and 100 m from an edge.

hear or observe any Blue-winged Warblers or hybrids (Brewster's or Lawrence's warblers) during our surveys.

There was a significant association between Golden-winged Warbler abundance and cover types within each of the 3 survey years and across all 3 years combined (Table 1). Golden-winged Warblers were most abundant in young aspen stands and least abundant in the swamp/mature edge habitat (Table 1, Fig. 2). Multiple comparisons showed that Golden-winged Warbler abundance in young aspen was significantly greater than abundance in thinned northern hardwoods and swamp/mature edges in 2004 and across all years combined. No significant differences were found between individual cover types within 2002 or 2003. We did not detect a temporal trend in abundance through the 3 survey years, either across all cover types ($P = 0.71$) or within individual cover types ($P > 0.40$); thus, we pooled the number of birds per station across years for analyses. There was an increase in the number of Golden-winged Warblers observed in some aspen stands as time since harvest increased from 1–2 years to 4–5 years. We observed a decline in Golden-winged Warbler observations in aspen stands that transitioned from 6–7 years since harvest to 9–10 years since harvest.

Our model evaluation with AIC_c at the stand scale (Table 2) indicated that aspen density was related to Golden-winged Warbler abundance across cover types. The top five models (M1–M5) had an AIC difference of <2. Models M6 and M7 had an AIC difference >2 and <3 with a likelihood estimate >0.23, and had less support than models with AIC differences <2. Models M1–M7 included aspen as one of their variables; the cumulative Akaike weight (wi) for density of aspen stems (0.98) was twice as high as the cumulative Akaike weight for any of the other variables in the models.

Station Scale.—One hundred and thirty of the 399 sampling stations had ≥0.50 birds/survey across all years and were 'used' in our analysis. The remaining 268 stations were 'unused' in our analysis. Models M1 and M2 had delta AIC of <2 (Table 3); both models contained the same three variables (aspen, ground vegetation, low woody cover). The remaining 13 models (Table 3) had less empirical support with AIC differences >6. Aspen was not the sole significant variable for predicting Golden-winged Warbler occurrence at the station scale. Aspen, ground vegetation, and low woody cover all had high cumulative Akaike weights (0.999, 0.989, and 0.975, respectively), and were positively related with Golden-winged Warbler use. Each of these weights was twice as high as cumulative Akaike weights for other variables in the model (alder stem density [0.345] and all other trees stem density [0.344]).

DISCUSSION

Given previous work in the Great Lakes Region, we were not surprised the young aspen cover type supported the greatest abundance of Golden-winged Warblers with over twice as many individuals as found in shrub swamp, northern hardwoods, and swamp/mature cover types. We were surprised that one jack pine stand had a particularly high density of Golden-winged Warblers. However, this stand was

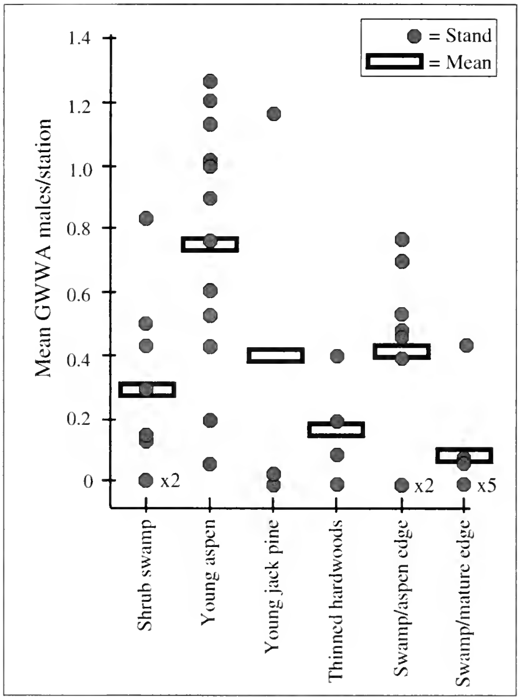

FIG. 2. Golden-winged Warbler males per station by cover type with individual stands and means in north central Wisconsin. (Males/station = maximum count from two same-season surveys averaged across 2–3 years and divided by number of point-count stations.)

unique because many of the Golden-winged Warblers were in the dense young aspen and deciduous brush that was encroaching along the edges of this stand, rather than in the less vegetated jack pine interior. Our sense is that in this Region, Golden-winged Warblers are often associated with brushy cover types and young aspen meets their needs.

We did not detect a change in abundance among years in any of the cover types but did find trends in certain individual stands. The increase in Golden-winged Warbler density observed as young (1–2 years since harvest) stands became older and the decrease in Golden-winged Warbler density observed as our relatively old (6–7 years since harvest) stands became older is indicative of the ephemeral nature of aspen habitat suitability for Golden-winged Warblers. Conditions were most suitable in 3–7 year-old regenerating aspen stands. These conditions likely produce the greatest number of aspen stems while at the same time allowing sufficient light to the ground layer to create the thick understory vegetation used by Golden-winged Warblers.

All regenerating aspen stands are not equal; we sampled a regenerating aspen stand on a sandy site for 3 years and observed no Golden-winged Warblers. This site was of such poor quality that number of aspen stems was significantly lower than at other sites. Further, there was a noticeable difference in the amount of woody cover and herbaceous cover at ground level. Young aspen stands appear to provide habitat for Golden-winged Warblers in northcentral Wisconsin, but some young aspen stands are not suitable where site conditions limit aspen stem densities and ground cover development.

Golden-winged Warblers associated with aspen and the amount of short woody and herbaceous vegetation. This thick understory cover is likely important as nest concealment. This may explain why we had an extremely difficult time locating Golden-winged Warbler nests within our stands. The three Golden-winged Warbler nests that we located all had an aspen overstory and were completely concealed by low woody and herbaceous cover.

We believe young aspen habitat may be a key cover type in north central Wisconsin for maintaining this species across this region. Young regenerating aspen cover may provide similar habitat to 'old field' habitat that is a key habitat for Golden-winged Warblers in the northeastern United States. Our results support the work of Confer et al. (2003) who reported a relationship between Golden-winged Warbler clutch sizes and abundance of shrub habitat <3.3 m high. However, our data reflect density estimates that may not be directly correlated with fitness (Van Horne 1983).

Our trends in abundance data supported the hypothesis that as regenerating stands of aspen and hardwoods become older, they become less suitable for Golden-winged Warblers. This was not the case for the swamp cover types, which did not show a consistent trend over the 3-year period; likely due to these stands changing little over time. Decline in habitat 'suitability' with stand age is further evidenced by reductions in Golden-winged Warblers in our older aspen (7–9 years of age) stands and increased abundance of Golden-winged Warblers in our younger aspen stands.

TABLE 2. Akaike Information Criterion (AIC) model selection at the stand scale using abundance of Golden-winged Warblers (males/station) as the response variable and 15 *a priori* habitat models as explanatory variables. Aspen and alder variables were the number of stems/m of each species at breast height, other consisted of the number of all other woody stems at breast height, low wood was the % of woody cover <1 m tall, and ground vegetation was the sum of the % cover of grass and low forbs. Models with delta AIC values of ≤2 are equally likely models.

Model	K	*n*	Variables	R^2	AIC (NEG)	AIC_c	Delta I (AIC_c)	Likelihood	wi	wi/wj
M1	2	43	ground vegetation, aspen	0.46	100.94	101.24	0.00	1.00	0.23	1.00
M2	3	43	low wood, ground vegetation, aspen	0.48	100.11	100.72	0.52	0.77	0.17	1.35
M3	1	43	aspen	0.43	100.62	100.72	0.52	0.77	0.17	1.35
M4	2	43	low wood, aspen	0.45	100.29	100.59	0.65	0.72	0.16	1.44
M5	2	43	alder, aspen	0.45	99.90	100.20	1.04	0.60	0.13	1.77
M6	3	43	other, alder, aspen	0.45	98.31	98.93	2.32	0.31	0.07	3.29
M7	5	43	other, low wood, ground vegetation, alder, aspen	0.48	96.66	98.28	2.96	0.23	0.05	4.60
M8	2	43	low wood, ground vegetation	0.34	92.04	92.34	8.90	0.01	0.003	76.67
M9	1	43	ground vegetation	0.29	91.13	91.23	10.01	0.01	0.002	115.00
M10	3	43	low wood, ground vegetation, alder	0.35	90.47	91.09	10.15	0.01	0.001	230.00
M11	2	43	ground vegetation, alder	0.30	89.85	90.15	11.10	0.004	0.001	230.00
M12	1	43	low wood	0.16	83.75	83.85	17.40	<0.001	<0.001	6,100.00
M13	2	43	low wood, alder	0.16	81.78	82.08	19.16	<0.001	<0.001	1.47E+4
M14	1	43	alder	0.003	76.46	76.59	24.68	<0.001	<0.001	2.56E+5
M15	1	43	other	0.001	76.343	76.440	24.80	<0.001	<0.001	2.76E+5

TABLE 3. Akaike Information Criterion (AIC) model selection at the station scale. The response variable for a station was 0 (unused) or 1 (used) dependent on whether the overall mean number of birds detected at a station over all years was ≤0.50 (unused) or >0.50 (used). Fifteen *a priori* habitat models were explanatory variables. Aspen and alder variables were the number of stems/m of each species at breast height, other consisted of the number of all other woody stems at breast height, low wood was the % of woody cover <1 m tall, and ground vegetation was the sum of the % cover of grass and low forbs. Models with delta AIC values of ≤2 are equally likely models.

Model	K	*n*	Variables	AIC (NEG)	Delta I (AIC)	Likelihood	wi	wi/wj
M1	3	399	ground vegetation, aspen, low wood	671.95	0.00	1.00	0.62	1.00
M2	5	399	low wood, ground vegetation, aspen, alder, other	669.81	1.19	0.55	0.34	1.81
M3	2	399	ground vegetation, aspen	665.26	6.69	0.04	0.02	28.36
M4	2	399	low wood, aspen	663.15	8.80	0.01	0.001	33.57
M5	1	399	aspen	659.52	12.43	0.002	0.001	206.12
M6	2	399	alder, aspen	659.44	12.51	0.002	0.001	214.54
M7	3	399	other, alder, aspen	658.03	13.92	0.001	0.001	434.19
M8	2	399	low wood, ground vegetation	643.37	28.58	<0.001	<0.001	6.62E+5
M9	3	399	low wood, other, ground vegetation	641.77	30.18	<0.001	<0.001	1.47E+6
M10	1	399	ground vegetation	624.54	47.41	<0.001	<0.001	8.12E+9
M11	2	399	ground vegetation, alder	622.56	49.39	<0.001	<0.001	2.18E+10
M12	1	399	low wood	614.29	57.66	<0.001	<0.001	1.37E+12
M13	2	399	low wood, alder	612.29	59.66	<0.001	<0.001	3.72E+12
M14	1	399	other	599.30	72.65	<0.001	<0.001	2.46E+15
M15	1	399	alder	598.33	73.62	<0.001	<0.001	3.99E+15

A specific example of a young stand becoming suitable is the Burrows Lake stand that had 2 birds in 2002 only 2 years after being harvested, 8 birds in 2003, and 15 birds in 2004 (4 years after harvest). We recorded 14 birds in 2002 at the Highway 155 study site 5 years after harvest, 14 birds in 2003, 6 birds in 2004, and only 2 birds in 2005, 8 years after harvest. This trend likely reflects changes in aspen stem density at the stand level and may not reflect changes in regional abundance of Golden-winged Warblers.

Golden-winged Warblers were present in a variety of cover types, but we suggest using differences in Golden-winged Warbler abundance is a useful way to prioritize habitat management actions. We suggest ranking cover types from most important to least important using density of young woody stems (<3 cm dbh). Further research to examine the correlation between Golden-winged Warbler abundance and fitness is needed to assure that abundance can be used as a surrogate for fitness (Van Horne 1983).

Shrub swamp supported significantly lower densities of Golden-winged Warblers than young aspen that results from clearcutting. However, this habitat may be an important component of the landscape for the persistence of Golden-winged Warblers over time because it occupies a relatively large portion of the land area in the Great Lakes Region (Michigan, Wisconsin, and Minnesota). Further, shrub swamp habitat seems to provide cover that supports low, static abundance of Golden-winged Warblers. An interesting question for future work is to address the influence of shrub swamp and other cover types on Golden-winged Warbler abundance at the landscape level.

Aspen forests in the Great Lakes Region have declined in total area since the 1930s, but remain the second most prevalent forest type. Aspen management is a primary means for managers in north central Wisconsin to create early seral habitat in the absence of fire and other natural disturbances (Hunter et al. 2001). Aspen management may be the most contentious issue on public forests in the Great Lakes Region (Cleland et al. 2001). Thus, management for Golden-winged Warblers at the landscape scale will require cooperation and coordination among many partners. Maintaining young aspen will likely increase the overall population of Golden-winged Warblers in north central Wisconsin if male Golden-winged Warbler density in young aspen is correlated with reproduction and fitness.

The relatively high densities of Golden-winged Warblers observed on our sites along with the absence of both Blue-winged Warblers and hybrids (Brewster's or Lawrence's warblers) are significant for Golden-winged Warbler conservation planning. Based on these two key factors, we recommend the northern portions of Wisconsin and Minnesota should be considered focal areas for Golden-winged Warbler conservation and management.

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ARTHROPOD PREY OF WILSON'S WARBLERS IN THE UNDERSTORY OF DOUGLAS-FIR FORESTS

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ABSTRACT.—Availability of food resources is an important factor in avian habitat selection. Food resources for terrestrial birds often are closely related to vegetation structure and composition. Identification of plant species important in supporting food resources may facilitate vegetation management to achieve objectives for providing bird habitat. We used fecal analysis to describe the diet of adult Wilson's Warblers (*Wilsonia pusilla*) that foraged in the understory of Douglas-fir (*Pseudotsuga menziesii*) forests in western Oregon during the breeding season. We sampled arthropods at the same sites where diet data were collected, and compared abundance and biomass of prey among seven common shrub species. Wilson's Warblers ate more caterpillars (Lepidoptera larvae), flies (Diptera), beetles (Coleoptera), and Homoptera than expected based on availability. Deciduous shrubs supported higher abundances of arthropod taxa and size classes used as prey by Wilson's Warblers than did evergreen shrubs. The development and maintenance of deciduous understory vegetation in conifer forests of the Pacific Northwest may be fundamental for conservation of food webs that support breeding Wilson's Warblers and other shrub-associated, insectivorous songbirds. *Received 28 April 2006. Accepted 23 February 2007.*

Food availability is a basic, critical habitat component that often limits reproductive success and survival of breeding birds (Martin 1987, Rodenhouse and Holmes 1992). Distribution and abundance of food have been correlated with population size of birds and are major factors in habitat selection and use (Wiens 1989, Block and Brennan 1993). The availability of food resources for terrestrial birds often is closely tied to vegetation structure and composition (Robinson and Holmes 1982, Holmes and Schultz 1988, Whelan 1989). Unfortunately, researchers rarely quantify direct linkages between vegetation and food resources (Holmes 1981), relying instead on correlative relationships between vegetation structure and bird density or abundance. These relationships can be obscure and unpredictable because birds do not usually respond directly to variables chosen by human observers to quantify habitat (Morse 1985). Thus, evaluation of habitat on the basis of vegetation structure may be unreliable unless associations between wildlife and vegetation are based on a detailed knowledge of species-specific resource requirements (Van Horne 1983). Direct measurements of resources, such as arthropod biomass available to insectivorous birds, may better predict habitat use than variables that describe vegetation (Brush and Stiles 1986). An understanding of the trophic pathways from vegetation to songbirds would provide an empirical foundation for management of vegetation to achieve objectives for managing bird habitat. The first step in understanding trophic links between birds and vegetation is to identify the composition of birds' diets. Once composition of the diet is known, it should be possible to identify plant species and habitat conditions that are important in supporting those food resources.

The goal of our study was to identify shrub species important in supporting arthropod prey for Wilson's Warblers (*Wilsonia pusilla*). We hypothesized that abundance of arthropod prey would differ among several of the most common plant species occurring in the understory of Douglas-fir (*Pseudotsuga menziesii*) forests. Our specific objectives were to: (1) identify the taxa and size categories of arthropods Wilson's Warblers use as prey, and (2) compare abundance and biomass of prey arthropods among common understory shrubs.

METHODS

Study Area.—Study sites were in forests of the Oregon Coast Range, in the Western Hemlock (*Tsuga heterophylla*) forest vegetation zone (Franklin and Dyrness 1988), between 200 and 500 m elevation. Mild, wet winters

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and dry summers characterize the regional climate. Sites were on lands managed by the Bureau of Land Management and the U.S. Forest Service. We sampled seven stands that were chosen to represent a range of variability in understory structure. All stands were dominated by Douglas-fir, but represented a range of ages and structural conditions. Four stands were relatively young, 55- to 65-years of age, and had regenerated naturally following clearcut harvesting. A single age cohort dominated the overstory of these stands with few (<1/ha) large trees and well-decayed snags persisting from previous stands. Three of these young stands had been thinned to uniform spacing 19–28 years prior to this study; the fourth remained unthinned. The remaining three stands had vegetation and structure typical of old-growth, as described by Spies and Franklin (1991). Major understory plant species included sword fern (*Polystichum munitum*), bracken fern (*Pteridium aquilinum*), salal (*Gaultheria shallon*), Oregon-grape (*Berberis nervosa*), vine maple (*Acer circinatum*), and oceanspray (*Holodiscus discolor*).

Diet Sampling.—We addressed our first objective by identifying the taxonomic groups and sizes of arthropods in fecal samples collected from adult Wilson's Warblers and comparing those to arthropods generally available on understory vegetation. We examined 87 fecal samples collected from 77 individual Wilson's Warblers that had been captured in mist-nets between mid-May and mid-July, 1996 and 1997. We identified arthropod fragments to the lowest taxonomic level possible using well-illustrated entomology texts and guides (Borror and White 1970, Shattuck 1985, Moldenke et al. 1987, Borror et al. 1989) and consultation with experts (A. R. Moldenke, Oregon State University; G. J. Brenner, Pacific Analytics Inc., Albany, OR). We measured lengths of whole femurs, tibias, and mandibles using an ocular micrometer fitted on the microscope. We estimated the original length of arthropod prey from fragments using regression equations developed from arthropods collected on shrubs in the Oregon Coast Range (Hagar 2004). We applied these regressions to whole tibias, femurs, and mandibles in fecal samples. We averaged predicted body lengths derived from femora and tibiae for spiders because we were frequently unable to distinguish spider femora from tibiae in fecal samples.

Arthopod Sampling.—Arthropods used to estimate available prey for Wilson's Warblers were collected from understory vegetation within 10 days of fecal sample collection in each stand, coinciding temporally and spatially with diet sampling. Arthropods (and fecal samples) were collected twice at each site between 26 May and 26 June, and between 30 June and 30 July. A shrub-beating method (Borror et al. 1989, Cooper and Whitmore 1990) was used to sample sedentary arthropods that are potential prey for Wilson's Warblers. Beating foliage to dislodge arthropods was an adequate method for sampling free-living, sedentary prey items available to birds, but organisms such as miners and borers were inadequately sampled because we did not visually inspect for organisms that may have been attached to vegetation. These organisms likely offer less food value to many species of insectivorous birds because of their relative inaccessibility and the increased effort required to forage on them effectively (Holmes and Schultz 1988).

We were logistically limited to sampling arthropods on vegetation ≤2 m above the forest floor. Wilson's Warblers are known to forage to the maximum height of the available vegetation (Stewart et al. 1977), but 75% of the foraging events observed on our study sites occurred in the layer of vegetation sampled for arthropods (Hagar 2004). However, we were unable to measure all prey available to Wilson's Warblers, and consulted the literature to evaluate the potential abundance of selected prey taxa in the forest canopy before making conclusions regarding prey availability and selection. We use "selection" to indicate that an arthropod group was used as prey more than expected based on frequency of occurrence in the environment.

"Shrub" refers to any woody plant species or fern having foliage within 2 m of the forest floor. Shrubs were selected for sampling at 50- to 75-m intervals along randomly established transects in each stand (Table 1). Species of vegetation sampled varied within and between stands because the two most dominant shrub species (based on percent cover) at each sampling point were selected for beating. Eight to 31 beating samples from each stand were col-

TABLE 1. Common and scientific names, and sample sizes (number of beating samples) of understory shrubs from which arthropod prey was sampled, Oregon Coast Range, 1996–99.

Common name	Scientific name	Acronym	*n*
Vine maple	*Acer circinatum*	ACCI	252
California hazel	*Corylus cornuta*	COCO	47
Salal	*Gaultheria shallon*	GASH	257
Oceanspray	*Holodiscus discolor*	HODI	61
Sword fern	*Polystichum munitum*	POMU	187
Bracken fern	*Pteridium aquilinum*	PTAQ	132
Western hemlock	*Tsuga heterophylla*	TSHE	156
Oregon-grape*	*Berberis nervosa*	BENE	7
Pacific dogwood*	*Cornus nuttalli*	CONU	1
Indian plum*	*Oemleria cerasiformis*	OECE	1
Douglas-fir*	*Pseudotsuga menziesii*	PSME	8
Thimbleberry*	*Rubus parviflora*	RUPA	1
Salmonberry*	*Rubus spectabilis*	RUSP	20
Snowberry*	*Symphoricarpos albus*	SYAL	3
Red huckleberry*	*Vaccinium parvifolium*	VAPA	3

* Sample size insufficient to include in comparison of prey load among plant species.

lected in each sampling period, depending on the size of the stand and the length of transect sampled. A different transect was established in each stand for each sample period within a year. Each shrub sample consisted of a surface area of ~1 m^2, corresponding to the size of the beating sheet. Thus, one sample of a shrub was approximately equal to 100 leaves (vine maple, oceanspray, and salmonberry [*Rubus spectabilis*]), 50 leaves (salal and California hazel [*Corylus cornuta*]), 5 fronds of bracken fern and 8 of sword fern, or a 1-m^2 branch (western hemlock). Arthropods were dislodged from clipped branches and foliage onto a canvas sheet and aspirated into vials. Plant material was dried and weighed.

We used an expanded sample of arthropods, collected over four summer seasons (May–Jul) 1996–1999 to describe differences in prey resources supported among shrub species. The sites represented were those used for collecting Wilson's Warbler diet data, plus six additional, similar stands in the same region of the central Oregon Coast Range (Doolittle 2000). We compared arthropod abundance among shrub species that were sampled in at least five stands and over at least 3 years.

Statistical Analyses.—The frequency of occurrence of each arthropod group in the diet was calculated as the number of fecal samples containing a given arthropod group divided by the total number of fecal samples. The lowest taxonomic levels that could be identified from fragments in fecal samples defined arthropod groups used for analyses. We calculated frequency of occurrence of each arthropod group from all beating samples (all shrub species pooled) collected in both years to derive a measure of available prey. We compared the frequency of occurrence of arthropod groups in the diet of Wilson's Warblers with frequency of occurrence on shrubs, and ranked groups by the ratio of frequency of occurrence in diet to that on shrubs. We used this forage ratio (Krebs 1989) as an index of prey selection by Wilson's Warblers with ratios >1 indicating greater than expected use based on availability in the understory. We focused analyses of prey sizes on arthropod groups that occurred in >60% of Wilson's Warbler diets and had forage ratios >1.

We used the Kolmogorov-Smirnov statistic (Steel and Torrie 1980) to test whether the distribution of arthropod sizes was the same for arthropods consumed by Wilson's Warblers as for arthropods collected from vegetation (PROC NPAR1WAY, SAS Institute 2000). We compared size distributions for larvae (including Lepidoptera [caterpillars] and Symphyta [sawflies]), Diptera (flies), Coleoptera (beetles), Homoptera, and all adult arthropods pooled. We used an *alpha* level of 0.05 for significance.

We compared the abundance (number of individuals/100 g dry plant matter) and biomass (arthropod weight [mg]/100 g dry plant matter) of arthropod groups identified as being selected as prey, based on the results of the diet analysis, among seven understory shrub species (Table 1). Arthropod weights were calculated from regression models that estimated wet weight based on body length (Hagar 2004). We pooled data across all 4 years to compare the abundance and biomass of five arthropod categories (adult beetles and flies >3 mm, adult Homoptera >2 mm, caterpillars >6 mm in length, and all arthropod prey combined) among plant species. The combined category of arthropod prey included adult flies and beetles >3 mm, caterpillars and sawfly larvae >6 mm, and all other adult arthropods >2 mm in length (except diplopods).

We used a Kruskal-Wallis non-parametric ANOVA with rank transformations (SAS Institute 2000) to test for differences in arthropod abundance and biomass among plant species for all prey groups except the category of combined taxa. We log-transformed response variables to normalize data and stabilize variances for the combined category of arthropod prey. A parametric ANOVA was used to test for differences in overall prey abundance and biomass among plant species (PROC MIXED, SAS Institute 2000). We evaluated overlap of 90% confidence intervals around back-transformed medians (all arthropod prey combined) or mean ranks (all other prey groups) to compare responses between specific plant species (Steidl et al. 1997). Significance was set at *alpha* = 0.05.

RESULTS

Arthropods in Diet.—We identified 15 groups of arthropod taxa in 87 Wilson's Warbler fecal samples from both years (Table 2). Nine families within four Orders also were identified from fragments: Homoptera: Achilidae, Aphididae, and Cercopidae; Neuroptera: Chrysopidae; Coleoptera: Cantharidae and Mordellidae; and Diptera: Empididae, Mycetophillidae, and Sciaridae. Caterpillars (Lepidoptera larvae), Homoptera, flies, and beetles had high frequencies of occurrence in fecal samples (>60%), and had forage ratios >1 (Table 2). Adult Lepidoptera and arthropod eggs had the highest forage ratios, but occurred relatively infrequently in the diet and were not well sampled by shrub-beating. In contrast, spiders occurred frequently, both in the diet and on vegetation.

TABLE 2. Arthropods in diets of Wilson's Warblers (n = 87) and on shrubs (n = 681 samples from beating) in the Oregon Coast Range, 1996–97. The ratio of the frequency of occurrence in diet to that on shrubs (forage ratio) is interpreted as an index of prey selection with ratios >1 indicating greater than expected use based on availability.

Group	Occurrence (%)		Forage ratio
	Diet	Shrubs	
Lepidoptera, adults	18	<1	45.98
Unknown arthropod eggs	14	1	11.49
Lepidoptera, larvae *	63	12	5.06
Homoptera (all taxa) *	86	51	1.69
Diptera *	99	59	1.67
Hymenoptera, wasps	46	28	1.67
Hymenoptera, Symphyta larvae	20	12	1.64
Coleoptera (all taxa) *	84	58	1.45
Homoptera, Cercopidae	23	16	1.44
Araneida (all spiders)	85	90	0.94
Neuroptera	5	7	0.67
Acari (mites)	2	20	0.11
Collembola	5	56	0.08
Psocoptera	2	31	0.07
Hemiptera	1	19	0.06

* Arthropod groups that occurred in > 60% of diets and had forage ratios >1.

Average size of adult arthropods consumed was ~4 mm and ranged from 2 to 10 mm (Fig. 1A). The size distribution of adult arthropods consumed differed (Kolmogorov-Smirnov two-sample test, $P < 0.001$) from the distribution for available adult arthropods indicating that Wilson's Warblers consumed prey that were larger than the most abundant items available. This pattern was consistently significant across the most frequently consumed adult arthropod groups (Kolmogorov-Smirnov two-sample test, $P < 0.001$, Fig. 1B–D). We did not find evidence of the largest available size classes (>12 mm) of adult arthropods, including flies, beetles, and spiders, in the diet.

Larvae, primarily caterpillars and sawflies, were the largest prey items consumed by Wilson's Warblers. Larvae ranged from ~6 to 26 mm in length. The size distribution of larvae consumed also differed (Kolmogorov-Smirnov two-sample test, $P < 0.001$) from that of available larvae because warblers were eating mostly the larger (>6 mm) larvae, which oc-

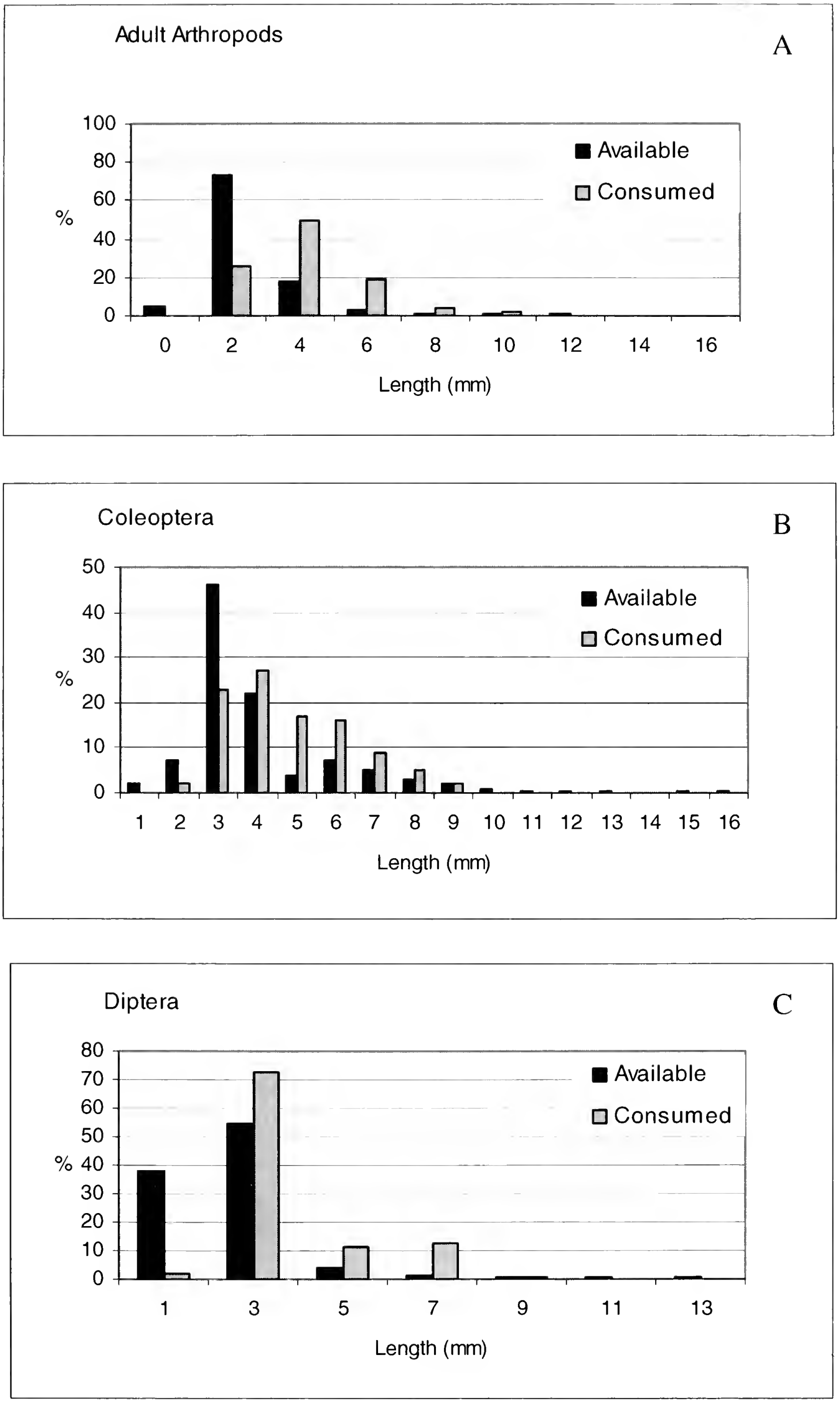
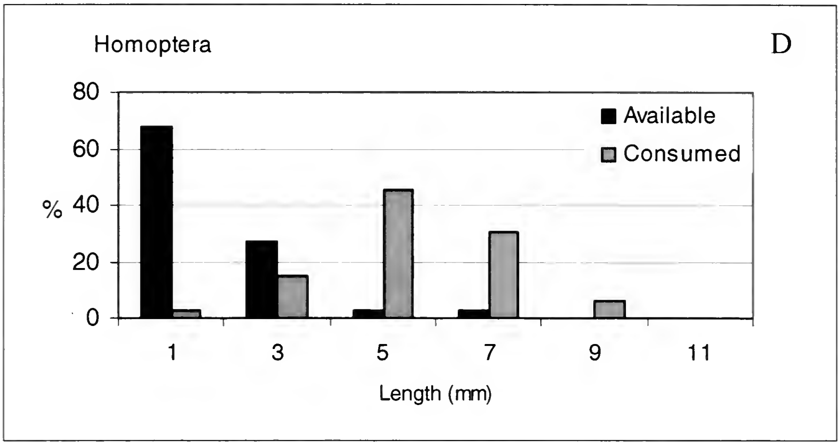


FIG. 1. Distribution among size classes of (A) adult arthropods, (B) Coleoptera, (C) Diptera, (D) Homoptera, and (E) sawfly and Lepidoptera larvae available as prey and those consumed by Wilson's Warblers in the Oregon Coast Range, 1996–1997.



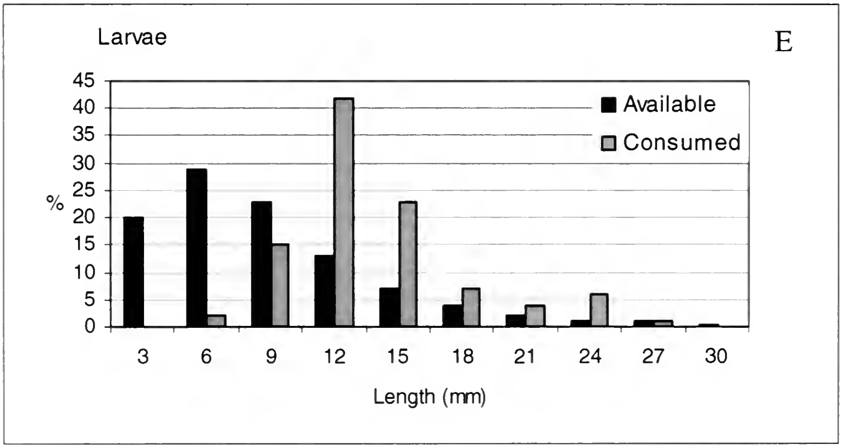


FIG. 1. Continued.

curred less frequently than those in the smaller size classes (Fig. 1E).

Arthropods in Understory Vegetation.—Thirteen insect Orders, seven non-insect arthropod taxa, and two mollusk taxa were identified from 28,438 individuals collected from 15 understory plant species over 4 years. The most abundant taxa overall were aphids and spiders, each accounting for more than 20% of the total number of individuals collected. Linyphiidae and Theridiidae, both web-spinning families, were the most abundant spiders.

Both abundance and biomass of all prey taxa combined varied significantly ($P < 0.001$, ANOVA) among plant species. Median prey abundance on bracken fern was more than 1.5 times greater than on any other species (Fig. 2A). Bracken fern also supported a higher biomass of prey than all plant species except oceanspray (Fig. 2B). Sword fern supported the second highest abundance of arthropod prey after bracken, but prey biomass was relatively low, reflecting the small size of most arthropods on this fern species. Western hemlock supported a lower abundance of prey than all other shrub species sampled, and biomass supported was lower than all except vine maple.

Caterpillars were rare on the vegetation we sampled, occurring in only 14% of the 1,136 beating samples across all shrub species. Abundance and biomass of caterpillars (>6 mm) differed (Kruskall-Wallis; abundance: $\chi^2_6 = 15.9$, $P = 0.01$, biomass: $\chi^2_6 = 12.9$, $P = 0.04$) among plant species. Oceanspray had a greater abundance and biomass of caterpillars

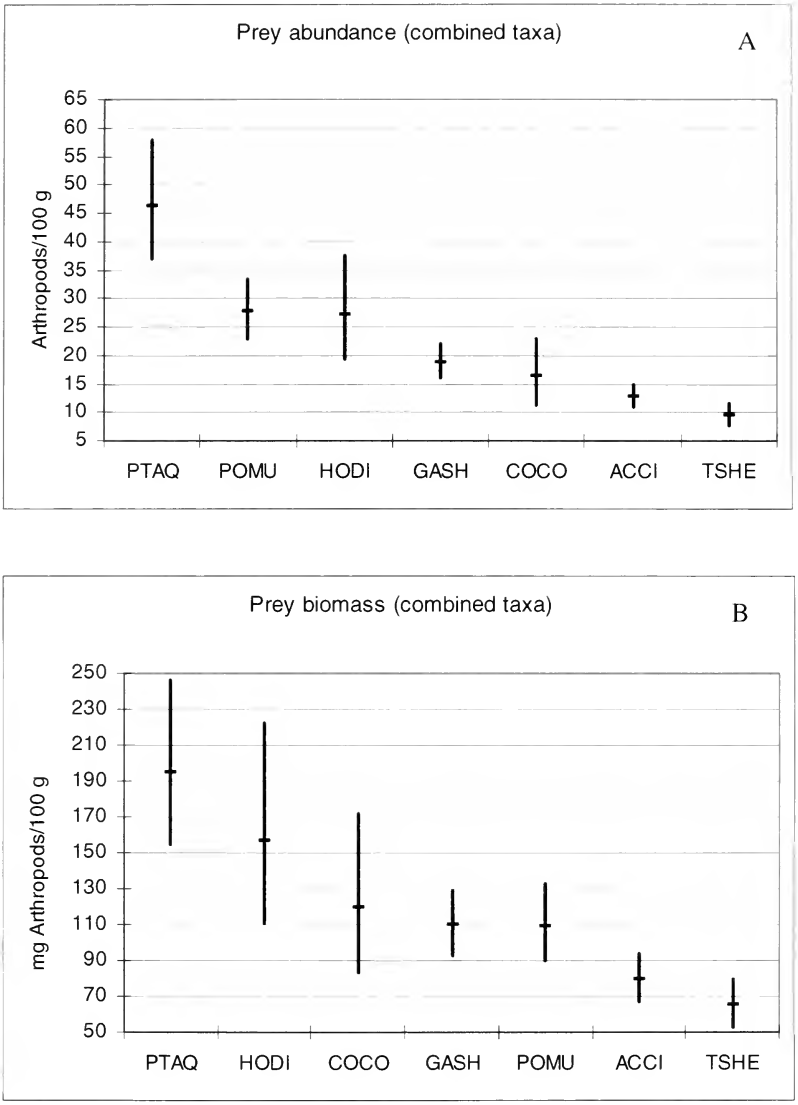


FIG. 2. (A) Median abundance index (individuals/100 g dry plant material) and (B) biomass index (mg/100 g dry plant material) with 90% confidence limits of arthropod prey for Wilson's Warblers (Coleoptera and Diptera >3 mm, larva >6 mm, and all other taxa >2 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in abundance or biomass if confidence limits of one do not overlap the median of the other.

than all other understory species except California hazel (Fig. 3). Hazel also had a relatively high rank for caterpillar abundance and biomass, although 90% confidence intervals overlapped mean values for vine maple and western hemlock. The frequency of occurrence of caterpillars also was higher on oceanspray (21%) and California hazel (36%) than on vine maple (16%), western hemlock (18%), bracken fern (11%), salal (9%), and sword fern (7%). Sword fern supported the lowest abundance and biomass of caterpillars of all plant species sampled (Fig. 3).

Abundance and biomass of flies (>3 mm) varied (Kruskall-Wallis: abundance: $\chi^2_6 = 16.1$, $P = 0.01$, biomass: $\chi^2_6 = 14.3$, $P = 0.03$) among plant species. Bracken fern and oceanspray ranked highest in abundance and

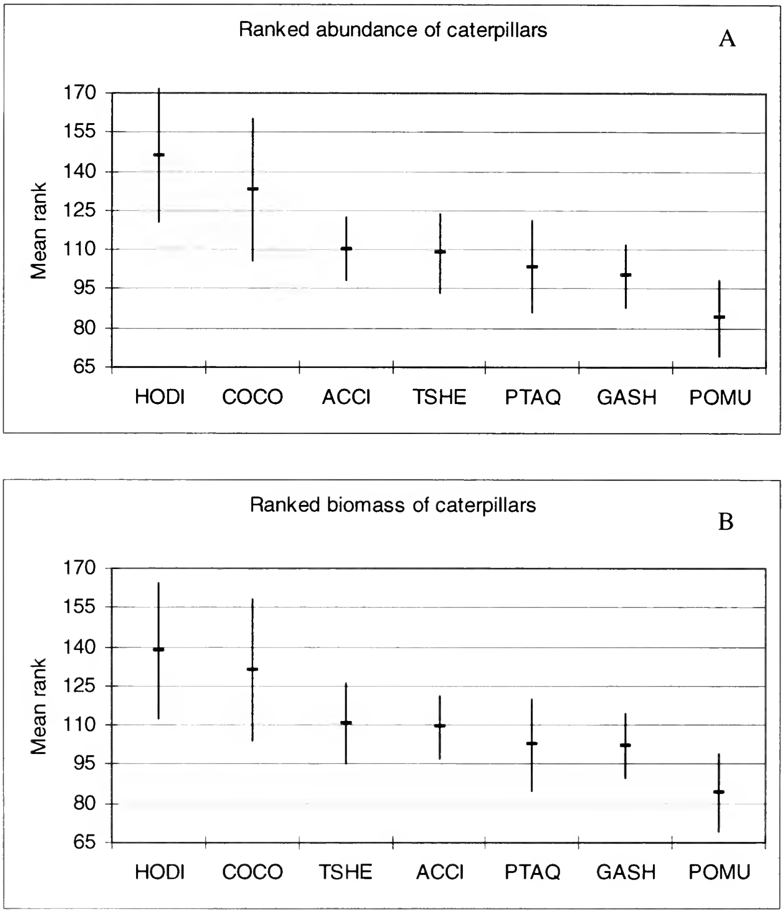


FIG. 3. (A) Ranked abundance and (B) biomass with 90% confidence limits of caterpillar (Lepidoptera larvae) prey for Wilson's Warblers on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

biomass of flies, but overlapping confidence intervals with vine maple, salal, and sword fern provided weak evidence of differences among these five species. Western hemlock and California hazel had the lowest rankings for both abundance and biomass of flies (Fig. 4).

Abundance and biomass of beetles (>3 mm) also differed (Kruskall-Wallis: abundance: $\chi^2_6 = 20.3$, $P < 0.01$, biomass: $\chi^2_6 = 16.1$, $P = 0.01$) among plant species. Western hemlock ranked lower for beetle abundance than all species except salal (Fig. 5), whereas California hazel, vine maple, oceanspray, sword fern, and bracken were all similar. Hazel ranked higher for biomass of beetles than all species except vine maple and oceanspray, whereas western hemlock, salal, sword fern, bracken, and oceanspray did not differ.

Homoptera abundance and biomass were clearly distinguished by plant species (Kruskall-Wallis: abundance: $\chi^2_6 = 49.4$, $P < 0.001$, biomass: $\chi^2_6 = 49.9$, $P < 0.001$) with bracken fern out-ranking all other plant species (Fig. 6). California hazel, salal, and sword fern ranked lower than bracken but higher than vine maple, oceanspray, and western hemlock in abundance and biomass of homopteran prey supported.

DISCUSSION

Wilson's Warbler Diet.—Breeding Wilson's Warblers preyed on a wide range of arthropod taxa, but consumed caterpillars, flies, beetles,

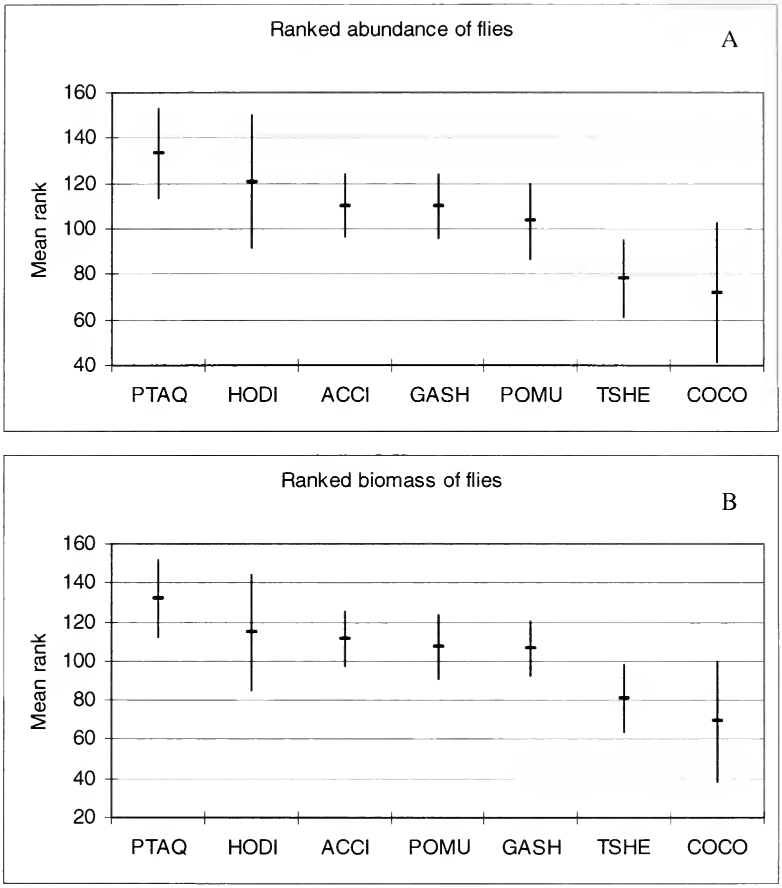


FIG. 4. (A) Ranked abundance and (B) biomass with 90% confidence limits of adult flies (Diptera >3 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

and Homoptera more frequently than expected based on availability. Caterpillars are known to be especially important prey for many neotropical migrant species that breed in temperate forests (Holmes et al. 1979, Graber and Graber 1983, Sample et al. 1993). Raley and Anderson (1990) also reported that caterpillars were an important component of Wilson's Warbler diets in montane willow (*Salix* spp.) habitats. Caterpillars and sawfly larvae have high calcium concentrations relative to many other arthropod groups (Schowalter and Crossley 1983), providing insectivorous birds with an essential resource for egg-laying. Caterpillar abundance and biomass have also been positively correlated with productivity and nestling growth rates of insectivorous birds (Holmes et al. 1992, Naef-Daenzer et al. 2000). Caterpillars probably represented an important source of energy and nutrition for birds on our study sites.

Active, flying insects such as adult flies and wasps likely were under-sampled with the foliage beating method we used to estimate available arthropod prey. Flies may have been more available than estimated in both understory and overstory vegetation, which would have caused an overestimate of the forage ratio. However, a large proportion of flies in the diet is supported by published accounts (Beal 1907, Ammon and Gilbert 1999) and reflects the hover-gleaning and aerial fly-catching foraging strategy frequently used by Wilson's Warblers (Bent 1953, Stewart et al. 1977). The selection of flies that we observed is consistent with the findings of Raley and Anderson

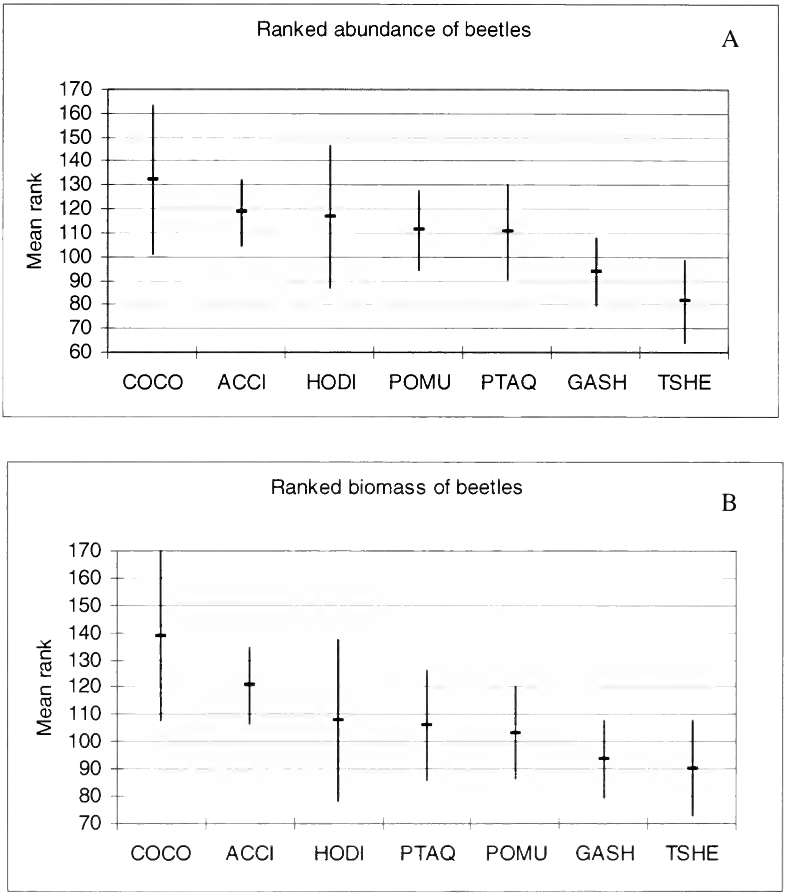


FIG. 5. (A) Ranked abundance and (B) biomass with 90% confidence limits of adult beetles (Coleoptera >3 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

(1990) for Wilson's Warblers foraging in montane willow habitats.

A high frequency of beetles in the diet relative to that on shrubs also is consistent with preferential selection of beetles as prey by Wilson's Warblers reported by Raley and Anderson (1990). We identified cantharid and mordellid beetles in warbler diets. Raley and Anderson (1990) also identified Cantharidae as a large proportion of beetles consumed by Wilson's Warblers. Mordellids are common on foliage but, unlike cantharids, they tend to move rapidly or take flight when alarmed (Borror and White 1970). We identified fragments of mordellids in only two of 87 Wilson's Warbler fecal samples.

Regardless of taxa, arthropods ≤2 mm in length were infrequent in diets of the birds we examined, even though this size class was abundant on understory vegetation. This is consistent with findings of Raley and Anderson (1990), who reported that Wilson's Warblers select prey >3 mm. Adult arthropods >12 mm in length also rarely occurred in the diet of Wilson's Warblers. However, adult arthropods that exceeded the maximum lengths in Wilson's Warbler diets were rare on the vegetation we sampled.

Distribution of Prey on Understory Plant Species.—Common understory plant species on our study sites varied in abundance and biomass of arthropod prey. Herbivorous insect species often are associated with a narrow range of plant taxa, which define characteristic assemblages of arthropods on each plant species (Schowalter 2000). We were not able to

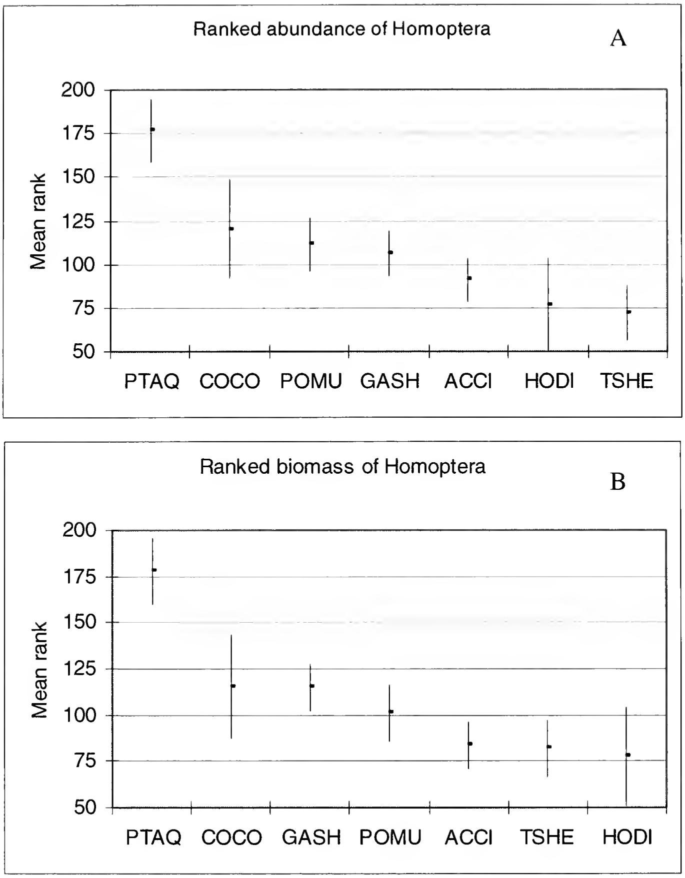


FIG. 6. (A) Ranked abundance and (B) biomass with 90% confidence limits of adult Homoptera (>2 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

identify most arthropods below the taxonomic level of family, but we found differences among plant species even for the coarser prey categories analyzed.

Plant species that ranked the highest for prey loads of arthropod taxa included oceanspray (caterpillars), California hazel (caterpillars and beetles), and bracken fern (combined prey taxa, flies, and Homoptera). Deciduous shrubs tended to rank higher for prey than evergreen shrubs. Others have noted the importance of deciduous shrubs and trees as foraging substrates (Morrison and Meslow 1983) and as sources of arthropod prey, particularly caterpillars, in conifer forests in the Pacific Northwest (Willson and Comet 1996). A large proportion of the Lepidoptera diversity in western forests is associated with deciduous trees and shrubs (Hammond and Miller 1998). Populations of forest insect species can fluctuate dramatically among generations, but prey diversity provides a stable resource for generalist insectivores over time (Jackson 1979). Oceanspray may be particularly important as a source of prey for birds because it supports both high diversity and high abundance of Lepidoptera (Muir et al. 2002). Western hemlock in the forest understory also was a potential source of caterpillars for birds, but supported low levels of all other prey.

Bracken, a fern that grows new fronds each spring from perennial rhizomes, supported a notably high abundance and biomass of all prey taxa pooled and Homoptera relative to other understory plants. Bracken fern supports a high abundance of herbivores and their associated predators (Lawton 1976), especially where it grows in large, dense patches in sun-lit areas (Doolittle 2000). In contrast, the evergreen fern species, sword fern, supported a relatively high abundance but low biomass of arthropods, reflecting an arthropod assemblage dominated by small detritivores such as Pscoptera and Collembola (Doolittle 2000) that were not important in bird diets. Few species of caterpillar are found on sword fern (Miller 1995).

CONSERVATION IMPLICATIONS

Insectivorous birds respond to spatial variation in arthropod availability among plant species (Johnson 2000) because foraging efficiency is likely maximized where prey density or biomass is highest (Royama 1970, Zach and Falls 1976, Whelan 1989). Our data indicate that broad-leaved deciduous shrubs and bracken fern provide optimal foraging habitat for breeding Wilson's Warblers because these plant species supported the highest abundance and biomass of foliage-dwelling arthropods ≥2 mm in length, particularly caterpillars, flies, beetles, and Homoptera.

Forest management has important effects on foraging habitat for Wilson's Warblers and other birds by influencing the structure and composition of vegetation communities. Traditionally, understory vegetation, particularly woody shrubs, has not been favored in management directed at timber production in the Pacific Northwest. The goal of standard vegetation management, using herbicides or manual methods, is to reduce cover of understory vegetation to minimize competition with crop trees (Burhill et al. 1989). Forest practice regulations require landowners to control competing vegetation as a means of ensuring successful conifer regeneration after clear-cut harvests (Oregon Department of Forestry 2006). Thus, shrub and hardwood tree cover in the Oregon Coast Range has declined over the past five decades (Kennedy and Spies 2004). Parallel declines in populations of shrub-associated bird species, including Wilson's Warbler, MacGillivray's Warbler (*Oporornis tolmiei*), and Swainson's Thrush (*Catharus ustulatus*) (Sauer et al. 2004) may be related to these regional changes in habitat.

Management goals for much of the federal forestlands in the Pacific Northwest have recently shifted from an emphasis on timber production to maintenance of ecosystems for a broader spectrum of products and services, including biodiversity and restoration of late-seral habitat. Managers plant or otherwise foster the growth of conifer regeneration in the understory, often after thinning or group-selection harvests, to encourage development of multi-layered forest stands (Tappeiner et al. 2002). Our results indicate that understory conifers contribute less to food resources for birds than a diverse assemblage including deciduous shrubs. Thus, a stand with deciduous shrubs in the understory is likely to be more functionally diverse than one with an understory composed of shade-tolerant conifers.

Our results indicate that deciduous vegetation is an important source of arthropod prey, especially caterpillars, which are preferred by Wilson's Warblers and other insectivorous birds. Forest management practices that maintain deciduous shrubs can help meet bird conservation goals. Furthermore, understory shrubs may serve an important function in maintaining the diversity of multiple taxa through associated food webs.

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DIETS OF BREEDING SOUTHWESTERN WILLOW FLYCATCHERS IN DIFFERENT HABITATS

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ABSTRACT.—We identified arthropods in fecal samples from 56 Southwestern Willow Flycatchers (*Empidonax traillii extimus*) at three localities in Nevada and Arizona with different plant communities during the 2004 breeding season. We concurrently collected arthropods in flight with Malaise traps and on different plant species by sweep net. These potential prey were identified to Order and counted. Fecal samples contained 57 taxa of spiders and insects including 32 families in 8 Orders. Flycatchers consumed similar diversities (numbers of taxa), but different taxonomic compositions (abundances in Orders) of arthropods among localities. Diets of *E. t. extimus* more closely resembled compositions of arthropods swept from plants than those trapped in flight with Malaise traps. Fecal samples at Upper Pahranagat Lake in southern Nevada contained arthropod compositions most related to those swept from *Salix gooddingii.* Fecal samples at the Virgin River near Mesquite in southern Nevada, where *Salix exigua* and naturalized *Tamarix ramosissima* grow, contained arthropod compositions most related to those swept from *S. exigua.* Fecal samples at Topock Marsh in western Arizona contained arthropod compositions most related to those swept from *T. ramosissima*, the dominant vegetation. The relation between flycatcher diet and arthropod composition on plants was least at Topock Marsh, suggesting prey from other communities are important in supplementing the fauna that develop on introduced *Tamarix.* The diverse diet of Southwestern Willow Flycatchers may take advantage of the increased nitrogen and sulfur contents of spiders and predaceous insects. *Received 26 July 2006. Accepted 13 January 2007.*

The Willow Flycatcher (*Empidonax traillii*) is a migratory passerine that breeds in northern and western United States and southern Canada, and winters in coastal areas from central Mexico to Panama (Sedgwick 2000). The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) is one of 4–5 subspecies distinguished primarily by plumage coloration and wing morphology (Phillips 1948, Unitt 1987, Browning 1993, Sedgwick 2000). It breeds from southern California east to western Texas and north to southern Utah (Browning 1993). *E. t. extimus* typically arrives in early May, begins nesting in early June, and lays 2–4 eggs/clutch (Unitt 1987). Willow Flycatchers produce several clutches each season, incubate eggs 13–15 days, and fledge young 11–16 days after hatch (Sedgwick 2000). Fall migration of Southwestern Willow Flycatchers occurs from early August to mid-September (Wang and Finch 1997).

Breeding Southwestern Willow Flycatchers require riparian habitat; willow trees (*Salix* spp.) predominate most breeding areas (Sogge et al. 2003) and are the most common nest site (Unitt 1987). Areas dominated by tamarisk (*Tamarix* spp.) also support breeding *E. t. extimus* (Sogge et al. 2003). Tamarisk is a shrubby tree native to Eurasia that has naturalized in the U.S. mostly as hybrids of *Tamarix ramosissima* and *T. chinensis* (Gaskin and Schaal 2002, 2003). Declining numbers of native riparian trees, concurrent with the spread of tamarisk, is a contributing factor in the decline in abundance of the Southwestern Willow Flycatcher and its resultant listing as endangered (USDI 1995).

Breeding Willow Flycatchers are generalist feeders that primarily consume arthropods, especially insects. Stomachs of Willow Flycatchers collected from across the species' range contained by volume mostly (41%) Hymenoptera followed by Coleoptera, Diptera, Lepidoptera, Hemiptera, fruits and seeds, Orthoptera, Odonata and Ephemeroptera, Araneae and Diplopoda, and Acari and Mollusca (Beal 1912). Most (73%) invertebrates delivered to nestlings in Ontario, Canada, were Hemiptera and Diptera but also included Mollusca, Arachnida, Isopoda, Orthoptera, Coleoptera, Hymenoptera, and Lepidoptera (Prescott and Middleton 1988). Prey in fecal samples from Southwestern Willow Flycatchers in southern California were mostly (78%)

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Araneae, Odonata, Hemiptera, Coleoptera, Hymenoptera, and Diptera (Drost et al. 2003).

Diets of *E. t. extimus* in separate breeding populations inhabiting different plant communities with dissimilar arthropod compositions have not been compared. Our objective was to quantify arthropod prey in fecal samples to compare diets at several localities with different plant species, including tamarisk, and to relate diets to abundances of arthropods trapped in flight or collected on plants. Specifically we were interested in four questions. (1) Does the diversity or taxonomic composition of arthropods eaten by flycatchers vary among different, geographically separated breeding populations? (2) Does the diversity or taxonomic composition of prey differ between adults (males and females) and young? (3) Are taxonomic compositions of arthropods eaten more related to those of arthropods collected on plants or trapped in flight? (4) Is flycatcher diet more related to arthropod compositions on native willows and poplars (*Populus* spp.) or on introduced tamarisk?

METHODS

Arthropods in flight and on plants, and fecal samples from *E. t. extimus* were collected at three localities. The Pahranagat Lake site (37° 19′ N, 115° 8′ W; elevation 1,010 m) was at the north shore of Upper Pahranagat Lake within Pahranagat National Wildlife Refuge in south-central Lincoln County, Nevada. The lake is an impoundment that receives water from springs. Riparian plants primarily are mature *Populus fremontii* and *Salix gooddingii* whose canopies extend over soil that is partially flooded during spring. The Virgin River site (36° 47′ N, 114° 6′ W; 460 m) was along the north edge of the Virgin River near Mesquite in northeastern Clark County, Nevada. Vegetation predominantly is *Salix exigua* and *Tamarix ramosissima* growing between the river and a shallow channel of flowing water. The Topock Marsh site (34° 49′ N, 114° 31′ W; 130 m) is a tamarisk-dominated area along the west shore of Topock Marsh, an impoundment next to the Colorado River, within Havasu National Wildlife Refuge in western Mohave County, Arizona. Vegetation surrounding riparian habitats at all three localities is mostly crops or pasture within the floodplain and Mohave desert scrub outside of the floodplain. Maximum temperature during July and minimum temperature during December average 36.8° and −3.5° C at Pahranagat Lake, 41.1° and −1.6° C at Virgin River (Bunkerville, NV), and 42.6° and 5.6° C at Topock Marsh (Needles, CA) (NOAA 2006).

Flying arthropods were collected with Malaise traps (Santee Traps, Lexington, KY, USA). Traps were placed in or at the edge of riparian stands inhabited by flycatchers. Two traps were placed at Pahranagat Lake, one within a stand of *P. fremontii* and one within an adjacent stand of *S. gooddingii*. One trap was placed at Virgin River at the edge of a mixed stand of *S. exigua* and *T. ramosissima*. One trap was placed at Topock Marsh within *T. ramosissima*. We collected arthropods with Malaise traps during five, 7–8 day trapping periods beginning on 5–6 May, 1 June, 17 June, 9 July, and 21 July 2004 at Pahranagat Lake and Virgin River, and 5 May, 2 June, 15 June, 6 July, and 20 July 2004 at Topock Marsh. Arthropods on plants near the Malaise traps were collected with a 38 cm-diameter, sailcloth sweep net on the last day of each trapping period. We sampled *P. fremontii* and *S. gooddingii* at Pahranagat Lake, *S. exigua* and *T. ramosissima* at Virgin River, and *T. ramosissima* at Topock Marsh. Each plant species was sampled with 100 sweeps along a transect flagged at both ends. The same plants, therefore, were swept on each date and we swept plants without regard to presence of flowers. Collected arthropods were stored in 70% ethanol, sorted to Order following Triplehorn and Johnson (2005), and counted. Numbers of arthropods in abundant taxa (>1,000 individuals) were estimated by counting individuals in subsamples delineated in a grid–lined Petri dish. Minute (<1 mm long) Hymenoptera (Cynipoidea, Proctotrupoidea, Ceraphoronoidea, and Chalcidoidea [except Chalcididae]) and nematocerous Diptera were not counted, because they were unlikely to be eaten by birds due to their size.

Fecal samples were collected into 70% ethanol during 15 May–9 August 2004 when birds, captured for banding or recaptured after previous banding, defecated. Birds were classified (nestling or adult) based on age and year when banded, and adults were classified to gender when possible (McLeod et al. 2005). Fecal samples came from different birds except for two samples from an adult male on 18 May 2004 at Topock Marsh. Fecal samples were classified into five collection periods approximating trapping intervals at each locality. Each collection period started the day trapping began and each period ended (except for the last period) the day preceding the next trapping period. Fecal samples at Pahranagat Lake were taken during only three of the collection periods (6–31 May, 17 Jun–8 Jul, and 21 Jul–6 Aug 2004).

Fecal pellets comprising samples were digested overnight in 10% KOH and neutralized with glacial acetic acid prior to examination through a stereo microscope. Small or medium-sized samples containing few arthropod parts were examined within a Petri dish. Identifiable arthropod parts in large samples, or abundant arthropod parts in small or medium-sized samples, were segregated into 5-ml scintillation vials to prevent repeatedly counting the same part. Arthropod parts were identified to the lowest taxon possible by comparing them with arthropods collected with Malaise traps and by sweeping plants, and with arthropods at the Bohart Museum of Entomology, University of California, Davis. The minimum number of individuals in each fecal sample was estimated by counting single body parts (e.g., head capsules, dorsal sclerites, ovipositors) and pairs of corresponding body parts (e.g., antennae, legs, wings). Arthropod parts from fecal samples and collected arthropods were deposited at the Bohart Museum. Images of identified arthropod parts are available at http://bohart.ucdavis.edu.

Diversity of arthropods in each fecal sample from *E. t. extimus* was measured by summing numbers of identified taxa and numbers of different, but unidentified, taxa. We averaged numbers of taxa in the two fecal samples from the same bird to enable all observations to be different birds. We compared numbers of taxa (transformed log[Y + 1]) among localities, among collection periods, and between nestlings and adults with ANOVA (version 10.2; SYSTAT, Richmond, CA, USA). Numbers of taxa (log[Y + 1]) were compared between adult males and females with an ANOVA that included locality and collection period as factors. Analyses weighted observations by the number of fecal samples.

Taxonomic compositions of arthropods in *E. t. extimus* fecal samples were quantified as abundances in Orders. We averaged abundances in Orders across the two fecal samples from the same bird. We compared abundances in Orders (log[Y + 1]) among localities, among collection periods, and between nestlings and adults by testing the interactions between Order and locality, Order and collection period, and Order and age class in an ANOVA that included Order, locality, collection period, and age class as factors. Gender of adults was similarly compared by testing the interaction between Order and gender in an ANOVA that included Order, gender, locality, and collection period as factors. Abundances of arthropods (log[Y + 1]) were compared among localities within each Order with ANOVA. If localities differed, we compared abundances between localities with lsd tests. Analyses weighted observations by the number of fecal samples.

Relations between taxonomic compositions in fecal samples and those in Malaise-trap or sweep-net samples were calculated at each locality. Fecal samples were paired with each trap sample and sweep sample from the same collection period. We regressed arthropod abundances in Orders (log[Y + 1]) in fecal samples against abundances in the same Orders (log[X + 1]) in all combinations of trap and sweep samples. Transformed abundances in fecal samples simultaneously related to more than one set of trap or sweep samples were plotted by adjusting means within collection periods with regression (Sokal and Rohlf 1969). Analyses weighted observations by the number of fecal samples.

RESULTS

More spiders and insects were caught by Malaise traps than by sweeping plants during collection periods when fecal samples were taken. Malaise traps ($\bar{x}$ ± SD, range) caught more (1,473 ± 1,519, 32–3,060; n = 3) arthropods within *P. fremontii* than within *S. gooddingii* (904 ± 308, 549–1,089; n = 3) at Pahranagat Lake, and more (13,236 ± 13,354, 6,661–37,089; n = 5) arthropods at Virgin River than at Topock Marsh (2,748 ± 968, 2,050–4,392; n = 5) per collection period. We swept fewer (68 ± 55, 14–124; n = 3) arthropods from *P. fremontii* and more (340 ± 414, 77–817; n = 3) from *S. gooddingii* at Pahranagat Lake, fewer (514 ± 270, 338–988;

n = 5) arthropods from *S. exigua* than from *T. ramosissima* (1,253 ± 948, 426–2,857; *n* = 5) at Virgin River, and fewer (138 ± 50, 72–193; *n* = 5) arthropods from *T. ramosissima* at Topock Marsh per collection period.

Fecal samples were collected from 56 *E. t. extimus*, 17 at Pahranagat Lake, 20 at Virgin River, and 19 birds at Topock Marsh. Fifty-seven taxa of spiders and insects, including 32 families, 15 genera, and 8 species, were identified in fecal samples (Appendix). Numbers of taxa in fecal samples from birds did not differ among localities (*F* = 1.5; df = 2, 48; *P* = 0.25) or among collection periods (*F* = 0.48; df = 4, 48; *P* = 0.75). Fecal samples ($\bar{Y}$ ± SD) from Pahranagat Lake contained 4.8 ± 1.9 (range = 2–9, *n* = 17) taxa, samples from Virgin River contained 4.6 ± 2.3 (range = 1–11, *n* = 20) taxa, and samples from Topock Marsh contained 3.7 ± 1.4 (range = 2–6, *n* = 19) taxa. Numbers of taxa in fecal samples did not differ between nestlings and adults (*F* = 0.05; df = 1, 48; *P* = 0.82). Fecal samples from nestlings contained 4.3 ± 2.0 (range = 1–8, *n* = 14) taxa, and fecal samples from adults contained 4.3 ± 1.9 (range = 2–11, *n* = 42) taxa. Numbers of taxa in fecal samples from birds also did not differ (*F* = 0.46; df = 1, 26; *P* = 0.50) between adult males and females. Fecal samples from males contained 4.3 ± 1.3 (range = 2–6, *n* = 22) taxa and fecal samples from females contained 5.2 ± 2.8 (range = 2–11, *n* = 13) taxa.

Two-hundred and ninety-six individual spiders and insects in eight Orders were found in fecal samples from *E. t. extimus* (Appendix). Taxonomic compositions of arthropods from fecal samples varied among localities (*F* = 4.2; df = 14, 384; *P* < 0.001) but did not vary among collection periods (*F* = 0.82; df = 28, 384; *P* = 0.74). We detected a weak, but non-significant, difference in taxonomic compositions between nestlings and adults (*F* = 1.8; df = 7, 384; *P* = 0.080). Taxonomic compositions did not vary between adult males and females (*F* = 0.20; df = 7, 250; *P* = 0.98).

Variation in taxonomic compositions of fecal samples among localities (Fig. 1) was evident when arthropod abundances were compared within each order. Arthropod abundances in fecal samples did not vary among localities in Araneae (*F* = 0.55; df = 2, 53; *P* = 0.58), Blattodea (*F* = 0.42; df = 2, 53; *P* = 0.66), Hemiptera (*F* = 2.4; df = 2, 53; *P* = 0.10), or Lepidoptera (*F* = 0.33; df = 2, 53; *P* = 0.72). Only one spider (Araneae) fragment was identifiable to family—a terminal leg segment with spatulate hairs characteristic of Anyphaenidae. The Blattodea collected were all specimens of the introduced cockroach *Blattella vaga* Hebard (Blattelidae). Leafhoppers (Cicadellidae) were the most abundant arthropod family in fecal samples (Appendix). Arthropod abundances in fecal samples varied among localities in Odonata (*F* = 4.3; df = 2, 53; *P* = 0.018), Coleoptera (*F* = 4.3; df = 2, 53; *P* = 0.018), Hymenoptera (*F* = 6.7; df = 2, 53; *P* = 0.003), and Diptera (*F* = 6.9; df = 2, 53; *P* = 0.002).

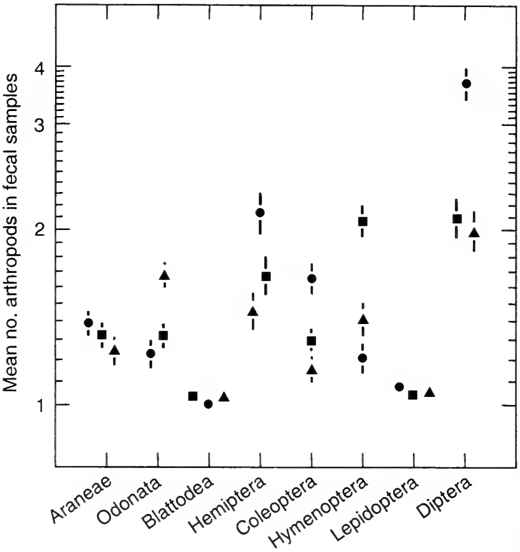

FIG. 1. Mean abundances (antilog $\overline{\log[Y + 1]}$) of arthropods by Orders in Southwestern Willow Flycatcher fecal samples. Circles = Pahranagat Lake, Nevada; squares = Virgin River, Nevada; triangles = Topock Marsh, Arizona. Vertical bars are ± SE's pooled within Orders. Overlapping symbols diagonally offset.

Odonata were more abundant in fecal samples at Topock Marsh than at Pahranagat Lake (*P* = 0.008) or Virgin River (*P* = 0.031). Odonata comprised 20% of arthropods in fecal samples at Topock Marsh and included dragonflies (Anisoptera) and damselflies (Zygoptera), distinguished by their large or small tarsal segments. Coleoptera were more abundant in fecal samples at Pahranagat Lake than at Topock Marsh (*P* = 0.005). Taxa consumed included a medium sized scarab (Scar-

TABLE 1. Linear regressions of arthropod abundances, transformed log(Y + 1), in Orders in Southwestern Willow Flycatcher fecal samples against abundances in the same Orders in sweep-net and Malaise-trap collections at three localities in southern Nevada and western Arizona.

Predictor variable[a]	B ± SE	F[b]	P	R^2
Pahranagat Lake				
Salix gooddingii sweep	0.17 ± 0.02	80.0	<0.001	0.37
S. gooddingii trap	0.12 ± 0.02	42.2	<0.001	0.24
Populus fremontii sweep	0.18 ± 0.03	35.7	<0.001	0.21
P. fremontii trap	0.034 ± 0.019	3.38	0.068	0.025
Multiple regression[c]				
S. gooddingii sweep	0.17 ± 0.02	83.7	<0.001	0.38
P. fremontii trap	0.036 ± 0.015	6.11	0.015	0.028
Virgin River				
Salix exigua sweep	0.11 ± 0.02	40.0	<0.001	0.20
Tamarix ramosissima sweep	0.086 ± 0.016	27.3	<0.001	0.15
S. exigua & *T. ramosissima* trap	0.073 ± 0.016	21.2	<0.001	0.12
Topock Marsh				
Tamarix ramosissima sweep	0.085 ± 0.020	17.5	<0.001	0.11
T. ramosissima trap	0.051 ± 0.014	13.6	<0.001	0.083

[a] Transformed log(X + 1); traps placed within, or at the edge of (Virgin River), plant species.
[b] Simple regression error df: Pahranagat Lake, 134; Virgin River, 158; Topock Marsh, 150.
[c] Model with each predictor variable $P < 0.05$ and highest total R^2 (0.40); error df = 133.

abaeidae) resembling a June beetle, weevils (Curculionidae), a medium sized Cerambycidae (*Aneflomorpha* sp.), and at least two species of Coccinellidae (*Olla v–nigrum* [Mulsant] and *Psyllobora* sp.). The most commonly consumed beetles were in the family Chrysomelidae; several fecal samples contained remains of the common species *Crepidodera opulenta* LeConte.

Hymenoptera were more abundant in fecal samples at Virgin River than at Pahranagat Lake (P = 0.001) or Topock Marsh (P = 0.017). Small bees (Halictidae) were the predominant Hymenoptera eaten, mostly at Virgin River, but ants also were found in several samples. Diptera were more abundant at Pahranagat Lake than at Virgin River (P = 0.003) or Topock Marsh (P = 0.001). Chironomidae and Syrphidae were the most abundant Diptera identified in fecal samples. Chironomidae were mostly found at Pahranagat Lake, while Syrphidae were mostly found at Topock Marsh. Syrphid flies consumed at Topock Marsh included *Copestylum pallens* (Weidemann), *Palpada alhambra* (Hull), and *Syritta pipiens* (Linnaeus). The most commonly eaten syrphid was *S. pipiens*. Species in two genera of Stratiomyiidae were consumed—*Myxosargus* sp. nr. *knowltoni* Curran and an unidentified species of *Sargus*. Other flies identified in fecal samples included *Ravinia* sp. (Sarcophagidae), *Ceroxys latisculus* (Loew) (Otitidae), and unidentified taxa of Chironomidae, Tachinidae, Scathophagidae, Tabanidae, and Dolichopodidae.

Relations between taxonomic compositions in fecal samples and those in Malaise-trap or sweep-net samples differed among localities. Taxonomic compositions of fecal samples at Pahranagat Lake were related to those in sweep samples of *S. gooddingii* and *P. fremontii* and trap samples within the stand of *S. gooddingii* (Table 1). Most variation in compositions of fecal samples at Pahranagat Lake (40%) was simultaneously related to compositions of arthropods swept from *S. gooddingii* and trapped within *P. fremontii* (Table 1, Figs. 2–3). Most of this variation (38%) was explained by arthropod compositions swept from *S. gooddingii*. Taxonomic compositions of fecal samples at Virgin River were related to those in sweep samples of *S. exigua* and *T. ramosissima*, and trap samples at the edge of both species (Table 1). Most variation in compositions of fecal samples at Virgin River (20%) was related to compositions of arthropods swept from *S. exigua* (Fig. 4). Taxonomic compositions of fecal samples at Topock

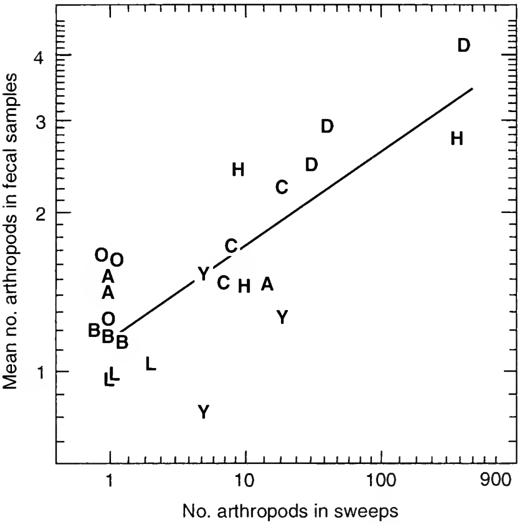

FIG. 2. Mean abundances (antilog $\overline{\log[Y + 1]}$) of arthropods in Southwestern Willow Flycatcher fecal samples during three collection periods, adjusted for arthropod abundances trapped within *Populus fremontii*, regressed against arthropod abundances ($X + 1$) swept from *Salix gooddingii* at Upper Pahranagat Lake, Nevada. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

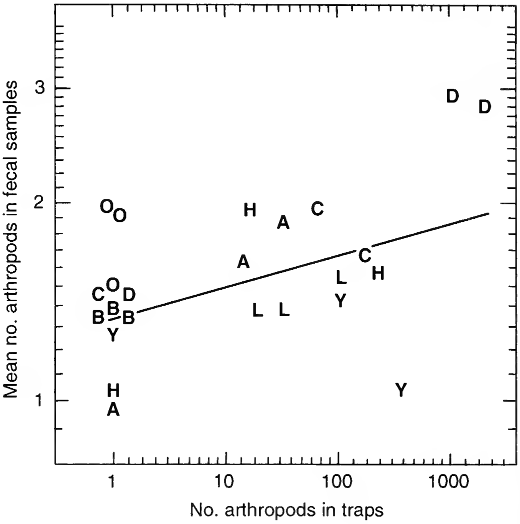

FIG. 3. Mean abundances (antilog $\overline{\log[Y + 1]}$) of arthropods in Southwestern Willow Flycatcher fecal samples during three collection periods, adjusted for arthropod abundances swept from *Salix gooddingii*, regressed against arthropod abundances ($X + 1$) trapped within *Populus fremontii* at Upper Pahranagat Lake, Nevada. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

Marsh were related to those in sweep and trap samples of *T. ramosissima* (Table 1). Most variation in compositions of fecal samples at Topock Marsh (11%) was related to compositions of arthropods swept from *T. ramosissima* (Fig. 5). The low percentage of explained variation at Topock Marsh partly was due to Odonata. Dragonflies and damselflies were found in fecal samples and captured ($n = 22$) in the Malaise trap but not caught by sweep net (Fig. 5). Compositions of fecal samples at Virgin River or Topock Marsh were not simultaneously related to more than one set of sweep or trap collections.

DISCUSSION

Breeding Southwestern Willow Flycatchers preyed upon a diverse variety of spiders and insects. Birds ate arthropods that were different in size, ranging from ladybird beetles (Coccinellidae) 2 mm in length to dragonflies 4 cm in length. Prey also differed in flight ability and included strong-flying dragonflies, and flower-visiting bees and non-flying ants (Formicidae). Spiders and insects from a variety of habitats were eaten. Prey included aquatic water boatmen (Corixidae), terrestrial spiders, arboreal leafhoppers, and ground-dwelling cockroaches.

Fecal samples with similar arthropod diversities, but different arthropod compositions, among breeding populations in different habitats suggest *E. t. extimus* adapt their diets to spiders and insects that are available. Individual birds at all three localities ate an average of four different taxa per fecal sample. This constant diversity in diet may result from birds eating a mixture of herbivorous and predaceous arthropods. Reproduction by insectivorous birds has been found to be affected by diet protein. For example, Blue Tits (*Parus caeruleus*) laid larger eggs when fed a high-protein diet and had larger clutches when provided with particular amino acids, such as sulphur-containing methionine (Ramsey and Houston 1997, 1998). Predaceous insects contain nitrogen concentrations averaging 15% higher than herbivorous insects; nitrogen con-

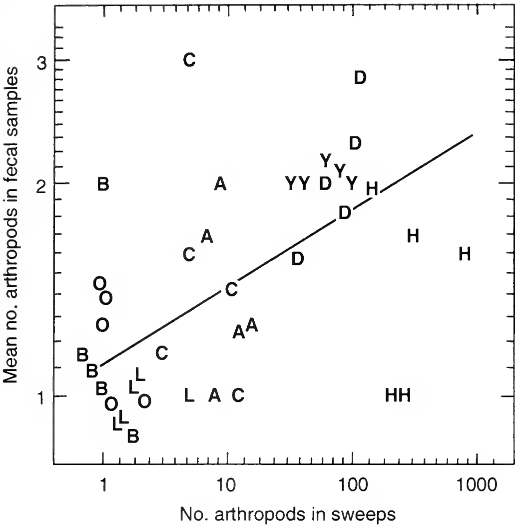

FIG. 4. Mean abundances (antilog $\overline{\log[Y + 1]}$) of arthropods in Southwestern Willow Flycatcher fecal samples during five collection periods regressed against arthropod abundances ($X + 1$) swept from *Salix exigua* along the Virgin River, Nevada. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

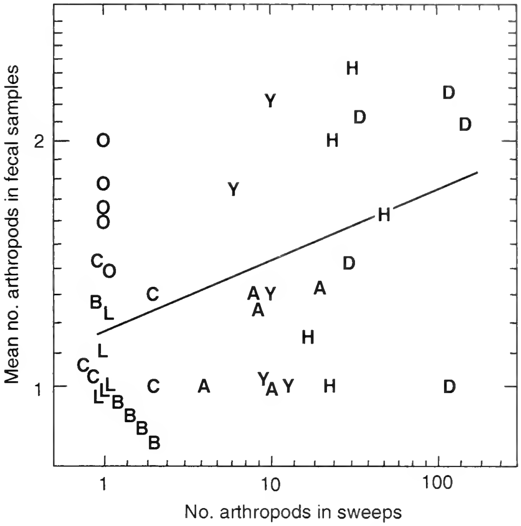

FIG. 5. Mean abundances (antilog $\overline{\log[Y + 1]}$) of arthropods in Southwestern Willow Flycatcher fecal samples during five collection periods regressed against arthropod abundances ($X + 1$) swept from *Tamarix ramosissima* at Topock Marsh, Arizona. A = Araneae; B = Blattodea; C = Coleoptera; D = Diptera; H = Hemiptera; L = Lepidoptera; O = Odonata; Y = Hymenoptera. Overlapping letters diagonally offset.

centrations are similar in predaceous insects and spiders (Fagan et al. 2002). Many arthropods eaten by Southwestern Willow Flycatchers were predaceous, including spiders, dragonflies, damselflies, ladybird beetles, and wasps (e.g., Vespidae and Sphecidae). Spiders also are rich in specific amino acids such as those containing sulphur (Ramsay and Houston 2003). Equivalent predation on spiders, comprising 7.4% of prey, at all three localities suggest they may have been eaten independent of abundance. More study and careful experimentation would be needed to demonstrate that flycatchers are augmenting their diets by preferentially selecting predaceous arthropods. If they do not, one must assume a random selection of a variety of arthropods supplies the required amounts of nutrients including nitrogen.

Our finding that similar diets are eaten by male and female adults concurs with the analyses by Drost et al. (2003) of fecal samples from breeding *E. t. extimus* in southern California. However, in contrast to our results, Drost et al. (2003) found nestlings ate a greater diversity of prey than did adults. These authors also found that diet compositions eaten by nestlings and adults differed with nestlings eating more Coleoptera and Odonata. Our data also suggests that nestlings and adults consume different compositions of spiders and insects, but this difference was small and difficult to detect. Diet shift during nestling development has been observed in Blue Tits and Great Tits (*Parus major*), with young (3–9 days of age) nestlings provided with more spiders (Cowie and Hinsley 1988). These authors suggest adults preferentially select spiders as food for young nestlings. Young nestlings may require specific amino acids provided by spiders (Ramsey and Houston 2003).

Compositions of arthropods in fecal samples show greater similarity to those collected by sweep net than to those collected by Malaise trap. This suggests that *E. t. extimus* forages more upon arthropods on plants than upon insects in flight. Willow Flycatchers glean, or fly and take prey from a substrate, and hawk, or fly and take prey that is in flight. Frequencies of these behaviors have been observed to vary by locality. Gleaning comprised 35 and 46% of foraging behaviors at two localities in Washington (Frakes and Johnson 1982) and 37 and 63% of foraging behaviors at two localities in Ontario, Canada (Barlow and McGillivray 1983). Frequencies of foraging behaviors may not equal frequencies of predation, because some foraging attempts likely are not successful. Insects in Orders we swept from plants may have been hawked. Hymenoptera and Diptera, common consumers of pollen and nectar, could have been hawked while flying between flowers. Conversely, insects in Orders caught in traps may have been gleaned. Dragonflies and damselflies land on plants but usually evade capture by sweep net.

The similarity between arthropod compositions in diets and what could be collected by sweeps or Malaise traps varied inversely with tamarisk's prevalence at each locality. The similarity was greatest at Pahranagat Lake, where native riparian trees are predominant, intermediate at Virgin River, where native *S. exigua* is mixed with naturalized *T. ramosissima*, and least at Topock Marsh, where *T. ramosissima* predominates. Greater prevalence of tamarisk appeared to result in lesser correspondence between predation by flycatchers and prey abundance. This suggests tamarisk provided a small proportion of arthropods eaten by flycatchers. Less predation on tamarisk arthropods is supported by the finding that arthropod composition in fecal samples at Virgin River resembled those on *S. exigua* more than *T. ramosissima*. However, abundances of these plants may have differed and influenced flycatcher diet.

Most arthropod biomass on *T. ramosissima* branches (98%) is comprised of only 2–3 herbivorous species, the armored scales *Chionaspis* spp. (Diaspididae) and the tamarisk leafhopper *Opsius stactogalus* Fieber (Cicadellidae) (Wiesenborn 2005). Armored scales are attached to plants and were not found in fecal samples from flycatchers. Tamarisk leafhoppers have been found in diets of several passerine species along the Colorado River in the Grand Canyon, Arizona (Yard et al. 2004). Populations of *O. stactogalus* are highly variable, spatially and temporally (Wiesenborn 2005) and likely provide an inconsistent food supply. *O. stactogalus* also would provide a relatively low source of nitrogen, consistent with other herbivorous Hemiptera (Fagan et al. 2002), because it appears to feed on phloem (Wiesenborn 2004). Predation by *E. t. extimus* on Hemiptera did not differ among localities despite different abundances of *T. ramosissima* and, expectedly, *O. stactogalus*.

Birds at Topock Marsh ate mainly Odonata and Diptera. The large size of Odonata, especially dragonflies, compared to other arthropods in fecal samples suggests they comprised a large proportion of arthropod biomass eaten by flycatchers at Topock Marsh. Dragonflies and damselfies are predaceous as aquatic nymphs and as terrestrial adults, and contain high nitrogen concentrations compared with other insects (Fagan et al. 2002). Most Diptera eaten by flycatchers at Topock Marsh were Syrphidae and may have been visiting tamarisk flowers. Immature syrphids are aquatic or terrestrial and typically predaceous or saprophagous (Vockeroth and Thompson 1987). Adult insects that immigrate into tamarisk after developing as immatures elsewhere, such as in the adjacent marshland or at its nutrient-rich edge, contribute significantly to the diet of breeding flycatchers at Topock Marsh. Immigrant predaceous insects seem to supplement *Tamarix*'s minimal arthropod food web and provide birds with nitrogen-rich food. Spiders and insects developing within or immigrating into *T. ramosissima* appear to supply adequate nutrition, because *E. t. extimus* breeding in tamarisk are not physiologically stressed (Owen et al. 2005).

CONSERVATION IMPLICATIONS

Preserving or restoring habitat for Southwestern Willow Flycatchers should strive to maintain or maximize overall arthropod abundance and diversity. Food availability in native habitats may be more effectively monitored by sweeping arthropods from plants than by capturing them with Malaise traps. However, an alternative method of sampling plant arthropods would be helpful, because sweeping can cause significant plant damage and disturbance. *Salix* spp., especially *S. gooddingii* and *S. exigua*, appear to be most effective in providing breeding *E. t. extimus* with arthropod food. Not all arthropods captured by flycatchers on or near *S. gooddingii* or *S. exigua* may have developed on these plants as immatures. Flying insects landing on *Salix* spp. may have been eating or gathering pollen or nectar, consuming honeydew, capturing prey, thermoregulating, or resting. An inadequate food supply produced by riparian habitats preserved or restored for *E. t. extimus* may need to be supplemented by immigrant insects, such as Odonata. Aquatic or other nonriparian habitats may be required to produce the abundance and diversity of arthropods needed to sustain populations of breeding Southwestern Willow Flycatchers.

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APPENDIX. Abundances of Arthropoda in fecal samples from Southwestern Willow Flycatchers in southern Nevada and western Arizona.

Order	Taxon below Order		*n*[a]
Araneae			19
	Tetragnathidae		2
	Anyphaenidae		1
Odonata			21
	Anisoptera		4
	Zygoptera		4
Blattodea	Blatellidae	*Blatella vaga* Hebard	2
Hemiptera			6
	Heteroptera		2
	Corixidae		4
	Miridae		3
	Cicadellidae		43
	Derbidae		1
Coleoptera			12
	Scarabaeidae		1
	Coccinellidae		4
		Olla v-nigrum (Mulsant)	1
	Cerambycidae	*Aneflomorpha* sp.	1
	Chrysomelidae		5
		Pachybrachis sp.	1
		Crepidodera opulenta LeConte	2
	Curculionidae		1
Hymenoptera			15
	Ichneumonoidea		2
	Braconidae		3
	Chrysididae		1
	Formicidae		5
		Pseudomyrmex sp.	1
	Pompilidae		1
	Vespidae		1
	Sphecidae		1
	Apoidea		5
	Halictidae		7
		Agapostemon sp.	2
Lepidoptera			4
	moths		1
Diptera			24
	Nematocera		7
	Chironomidae		31
	Stratiomyidae	*Sargus* sp.	1
		Myxosargus sp. nr. *knowltoni* Curran	1
	Tabanidae		1
	Dolichopodidae		1
	Syrphidae		5
		Copestylum pallens (Weidemann)	4
		Palpada alhambra (Hull)	2
		Syritta pipiens (Linnaeus)	13

APPENDIX. Continued.

Order	Taxon below Order		n^a
	Acalyptratae		2
	Otitidae		2
		Ceroxys latiusculus (Loew)	1
	Ephydridae	*Ochthera mantis* (DeGeer)	2
	Drosophilidae		1
	Scathophagidae		1
	Calyptratae		4
	Calliphoridae		1
	Sarcophagidae	*Ravinia* sp.	2
	Tachinidae		1

[a] Abundances of higher taxa do not include those of lower taxa.

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PREY USE AND PROVISIONING RATES OF BREEDING FERRUGINOUS AND SWAINSON'S HAWKS ON THE SOUTHERN GREAT PLAINS, USA

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ABSTRACT.—We collected diet data at 12 Ferruginous Hawk (*Buteo regalis*) and 14 Swainson's Hawk (*B. swainsoni*) nests in a short-grass prairie and agricultural community in the panhandle area of northwest Texas and southwest Oklahoma, and in northeastern New Mexico during the 2003–2004 breeding seasons. We documented 959 Ferruginous Hawk and 1,058 Swainson's Hawk prey deliveries during ~5,618 hrs of video monitoring. Ferruginous Hawks delivered 10.0 ± 0.7 ($\bar{x}$ ± SE) prey species per nest and typically larger prey. Swainson's Hawks delivered 13.4 ± 1.1 prey species per nest and typically smaller prey. There was a dietary overlap (Simplified Morisita Index [C_H]) of 0.31 in prey species delivery frequency and 0.56 in prey species' biomass. Ferruginous Hawks made 4.6 deliveries/day at 480 g/delivery whereas Swainson's Hawks delivered smaller prey items (147 g/delivery) but more frequently (7.0 deliveries/day). Deliveries/day and mass/day increased with increasing brood sizes of both species, but deliveries/day/nestling and mass/day/nestling decreased. Provisioning rates did not vary significantly over the nestling period. These data represent the most accurate diet quantification to date for Ferruginous and Swainson's hawks. Ferruginous Hawks used a larger array of prey types than shown in other studies based on indirect diet analysis methods. The low interspecific diet overlap suggests that prey is partitioned, which may facilitate the well-documented sympatric distribution of the two species. *Received 31 August 2006. Accepted 23 December 2006.*

Food and feeding habits are among the most fundamental components of animal ecology (Errington 1935). Initial studies of raptor diets were directed at assessing impacts of depredation on game species and livestock (Errington 1930). More recent studies provide information on raptor niches in relation to community structure, and on the availability and distribution of prey species (Johnson 1981, Marti 1987). Prey availability and composition can affect all aspects of raptor species ecology including population trends (Newton 1979, Woffinden and Murphy 1989, Cully 1991, Olsen 1995). Thus, quantifying and understanding diets is an essential component for successful management and conservation of raptor species.

Ferruginous Hawks (*Buteo regalis*) and Swainson's Hawks (*B. swainsoni*) are often sympatric in grasslands, shrub-steppe, and deserts (Bechard and Schmutz 1995, England et al. 1997). Both species have experienced population declines, primarily due to habitat conversion and degradation, but also from persecution and secondary pesticide poisoning (Schmutz and Fyfe 1987, Houston and Schmutz 1995, England et al. 1997). Research on sympatric Ferruginous and Swainson's hawk populations has been limited to the northern and western regions of their breeding distribution. Most studies have focused on interspecific comparisons of nest site selection, distribution, productivity, and success but also on diet composition and responses to prey fluctuations, and effects of anthropogenic activities (Thurow and White 1983, Steenhof and Kochert 1985, Schmutz and Hungle 1989, Cully 1991, Restani 1991).

Diets of Ferruginous Hawks are monotypic compared to the more generalist diet of Swainson's Hawks (Bechard and Schmutz 1995, England et al. 1997). Jackrabbits (*Lepus* spp.) tend to be the dominant prey of Ferruginous Hawks west of the Continental Divide whereas ground squirrels (*Spermophilus* spp.) and prairie dogs (*Cynomys* spp.) are dominant

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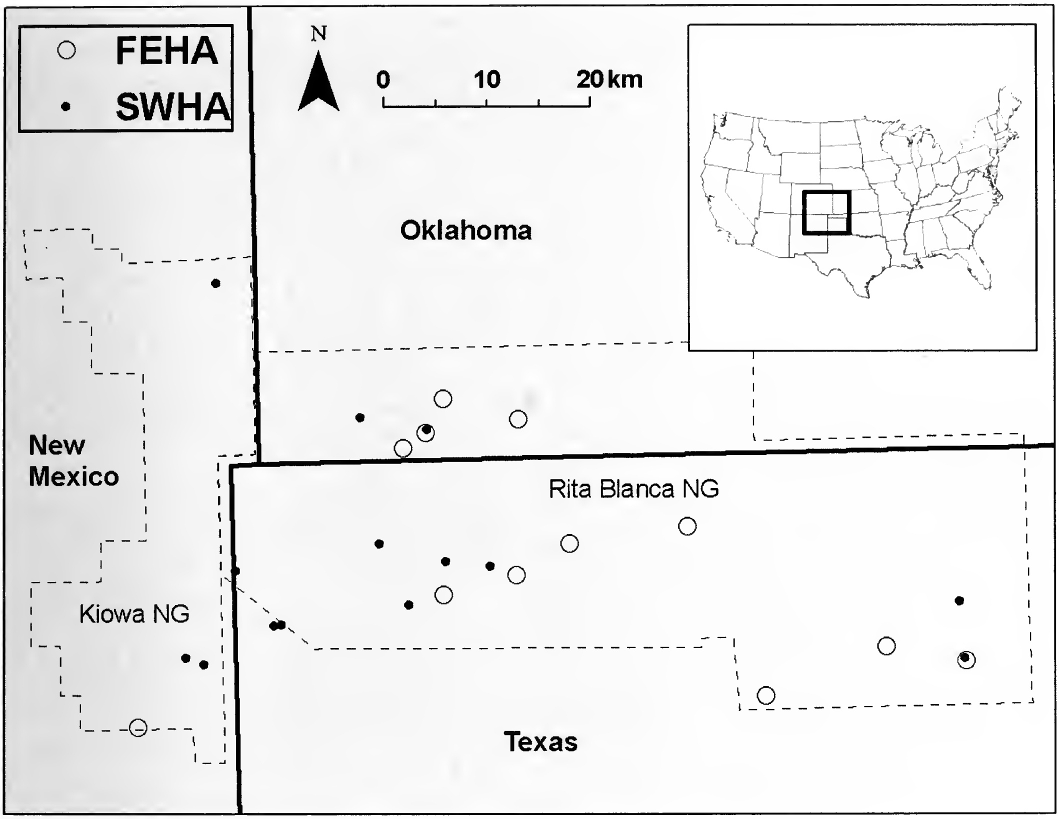

FIG. 1. Study area and distribution of 12 Ferruginous Hawk nests (FEHA) and 14 Swainson's Hawk nests (SWHA).

prey to the east (Bechard and Schmutz 1995). Prairie dogs are an important, if not critical, prey item for migrating and wintering Ferruginous Hawks in Texas and adjacent states (Schmutz and Fyfe 1987, Cully 1991, Allison et al. 1995, Plumpton and Andersen 1997). The availability of prairie dogs appears to have induced Ferruginous Hawks to forage and over-winter in heavily cultivated areas of Texas (Schmutz and Fyfe 1987) and fragmented suburban areas of eastern Colorado (Plumpton and Andersen 1998).

The importance of prairie dogs as prey for breeding Ferruginous and Swainson's hawks has not been well investigated. Furthermore, breeding season diets of Ferruginous Hawks in the southern extent of their range are mostly unknown. The potential use of black-tailed prairie dogs (*Cynomys ludovicianus*) or species associated with prairie dog colonies (Kotliar et al. 1999) by Swainson's Hawks has also not been investigated. An understanding of the potential relationships between black-tailed prairie dogs and these two raptor species is important because prairie dogs have been and continue to be subject to extensive eradication efforts throughout their range, and have experienced an estimated 98% population decline (Kotliar et al. 1999).

The overall objective of this study was to quantify the breeding season diets of coexisting Ferruginous and Swainson's hawk populations. Our specific objectives were to: (1) identify the prey species of both hawk species in terms of delivery frequency and biomass, (2) examine dietary breadth and overlap, (3) compare daily provisioning rates, and (4) evaluate the effects of brood size and nestling age on prey provisioning.

METHODS

Study Area.—The study area (Fig. 1) encompassed the U.S. Forest Service Rita Blanca National Grasslands in Dallam County, Texas and southern Cimarron County, Oklahoma, and the eastern section of the Kiowa National Grasslands in Union County, New Mexico and adjacent private property where access was permitted (36° 20′ N, 102° 40′ W). This tri-state area is within the Southern Great Plains Region with elevations ranging from 1,144 to 1,558 m. The historical plant community type is short-grass prairie, the driest of the mid-continental grasslands (Brown 1985), and sporadic droughts are common in the region (Samson et al. 2004). Warm, dry summers and cold, dry winters are typical of the study area with Dallam County, Texas, receiving an average of 18.6 cm of precipitation annually, most of it from April to August (National Weather Service 2004).

The national grasslands included in this study encompassed ~81,000 ha of various sized tracts of short-grass and mixed-grass prairie interspersed among private property holdings. They supported cattle grazing, outdoor recreation, and wildlife management (U.S. Department of Agriculture 2004). The adjacent private property supported agricultural crops such as corn, sorghum, and wheat, cattle ranching, and a variety of range management and conservation programs.

Common vegetation included warm- and cool-season grasses such as *Bouteloua* and *Elymus* spp., buffalo grass (*Buchloe dactyloides*), silver bluestem (*Bothriocloa laguroides*), and other species including sagebrush (*Artemisia* spp.), plains yucca (*Yucca angustifolia*), buffalo gourd (*Cucurbita foetidissima*), and plains sunflower (*Helianthus petiolaris*). Trees and woody shrubs were sparse and consisted primarily of crop, road, and residence shelterbelts. Tree species included Siberian elm (*Ulmus pumila*) and plains cottonwood (*Populus deltoids occidentalis*). Less common species included Russian olive (*Elaeagnus angustifolia*), eastern red cedar (*Juniperus virginiana*), and black locust (*Robinia psuedoacacia*).

Nest Selection and Video-monitoring.—We located breeding Ferruginous Hawk and Swainson's Hawk pairs by visiting known nest sites (unpubl. data), and conducting road surveys during courtship and incubation periods beginning in March for Ferruginous Hawks and April for Swainson's Hawks. We assessed the status of nests from a distance with optics and an extendable mirror-pole at the nest site. We considered an area occupied by a breeding pair of hawks if an adult pair was present at the nest site and nest-building, or if eggs or nestlings were present.

We used video-recording systems (Giovanni 2005) to document prey deliveries at a different sample of Ferruginous Hawk and Swainson's Hawk nests each year. We randomly selected nests for video-monitoring but logistical restraints (i.e., private property access and unsafe nest substrates) prevented us from using some of the initially selected nests. We installed video systems during the nestling period and moved video systems to a new nest site after failure or fledging of young at the initial nest. We programmed the systems to record from 0630 to 2130 hrs CDT at 72-hr (1.3 frames/sec) and 48-hr (0.8 frames/sec) speeds (Smithers et al. 2005). This allowed recording 3–4 days of 15-hr daylight intervals on a single 2-hr tape. We changed videotapes and batteries twice each week to insure continuous video coverage.

We attempted to identify prey items to the lowest taxonomic level possible. We categorized delivered prey as unknown when no image of the item was visible but a delivery was evident based on behavior of the hawks. We grouped eastern (*Sylvilagus floridanus*) and desert (*S. audubonii*) cottontails, and yellow-faced (*Cratogeomys castanops*) and plains (*Geomys bursarius*) pocket gophers into single, generic prey types (i.e., "cottontails" and "pocket gophers"). We assumed all grasshopper deliveries to be plains lubber grasshoppers (*Brachystola magna*) (Pfadt 1994).

Age and Mass Estimates.—We estimated age and biomass of mammalian prey based on relative size. For instance, juvenile black-tailed prairie dogs and black-tailed jackrabbits (*Lepus californicus*) were visibly smaller than their adult counterparts. We assumed prey to be adult age when it was not clearly juvenile. We also assumed avian prey to be of adult status unless juvenile plumage was detectable.

We used the mean mass of males and females for non-sexually dimorphic prey species. We used the mean of mass estimates for eastern and desert cottontails, and also for yellow-faced and plains pocket gophers. We obtained other mammal mass estimates from Davis and Schmidly (1994), Best (1996), and Hoogland (1996). We obtained mass estimates for bird prey from Dunning (1984), plains lubber grasshoppers from Schell et al. (1994), snake species from measurements taken at fortuitous encounters within the study area (Giovanni 2005) and museum specimens, Texas horned lizards (*Phrynosoma cornutum*) and Great Plains skinks (*Eumeces obsoletus*) from unpublished data, and birds, frogs and toads, rodents, lizards, and snakes not identified to species from Steenhof (1983).

Some prey deliveries were unidentifiable due to immediate ingestion or obstructed viewing during feeding. We estimated biomass for unidentifiable prey (to calculate prey provisioning rates) by calculating a mean mass of the less conspicuous but frequently delivered prey species (e.g., grasshoppers for Swainson's Hawks).

We assumed that adult males fed away from the nest, as suggested by their frequent delivery of partial prey items and minimal time at the nest. Ascertaining if the adult female was feeding in concert with nestlings was difficult due to the time-lapsed recording and resolution of the video footage. We were also restricted from identifying if digestive tracts were ingested because of limited video resolution. We made no assumptions addressing the ingestion of foods in digestive tracts of prey and considered delivered prey an index of ingested food.

Delivery Rate Analyses.—We calculated prey delivery frequency and provisioning as deliveries/day and deliveries/nestling/day. We estimated g/delivery, g/day, and g/nestling/day for biomass delivery analysis. We also examined patterns of delivery rates among nests with different brood sizes and temporal patterns in prey delivery rates across the nestling growth period. We estimated hatching dates by backdating from nestling age estimates (Moritsch 1983, 1985) of the oldest nestling (Warnke et al. 2002), and used delivery rate data up to fledging ages of 50 days for Ferruginous Hawks (Bechard and Schmutz 1995) and 45 days for Swainson's Hawks (England et al. 1997). We used 5-day nestling age intervals to standardize prey provisioning rates across the nestling period. We calculated g/hr and g/nestling/hr by summing delivered prey biomass within the 5-day age intervals, and then dividing by the total hours of video footage for the intervals and nestling number.

Statistical Analyses.—We used Statistica 6.1 (StatSoft, Inc. 2003) for data analyses and all tests were conducted at an *alpha* level of 0.05. We attempted to correct data having non-normal experimental error distributions with appropriate transformations (Zar 1999). We tested for homogeneous variances among treatments with Levene's test when normality was satisfied (Zar 1999). We then tested for interspecific differences with a *t*-test for independent samples by group (i.e., group 1 being Ferruginous Hawks and group 2 being Swainson's Hawks) or with a one-way ANOVA (Zar 1999). We used the nonparametric equivalents when transformations failed to normalize data (Zar 1999).

We made interspecific comparisons of percent delivery frequency and biomass of black-tailed prairie dogs, mammals, mammals weighing >200 g, birds, reptiles and amphibians, grasshoppers, diet richness, and diet breadth. We also examined interspecific provisioning rates on the basis of deliveries/day and g/day. We examined deliveries/nestling/day and g/nestling/day to examine possible influences of brood size on provisioning rates. We used repeated-measures ANOVA (Zar 1999) to compare nestling provisioning rates across time by measuring deliveries/hr and deliveries/nestling/hr, and g/hr and g/nestling/hr with pooled diet data from 5-day intervals based on nestling age. We used Smith's Measure of Niche Breadth (*FT*) (Smith 1982) to calculate dietary breadth, and the Simplified Morisita Index (C_H) (Krebs 1999) to calculate interspecific prey species' delivery frequency and biomass overlap. We reported comparative data as means and standard errors.

RESULTS

Ferruginous Hawk Food Habits.—We video-monitored six Ferruginous Hawk nests in 2003 and six different nests in 2004, and assumed all nesting pairs (12) to be different and independent between years. We recorded 3,231 daylight hrs ($\bar{x}$ = 269 ± 44 hrs/nest) of video footage, and identified 740 of 937 (79%) prey items to species, genus, or family.

Rodents and rabbits dominated Ferruginous Hawk diets, comprising 73.2% of the prey and 81.7% of the prey biomass delivered to nests.

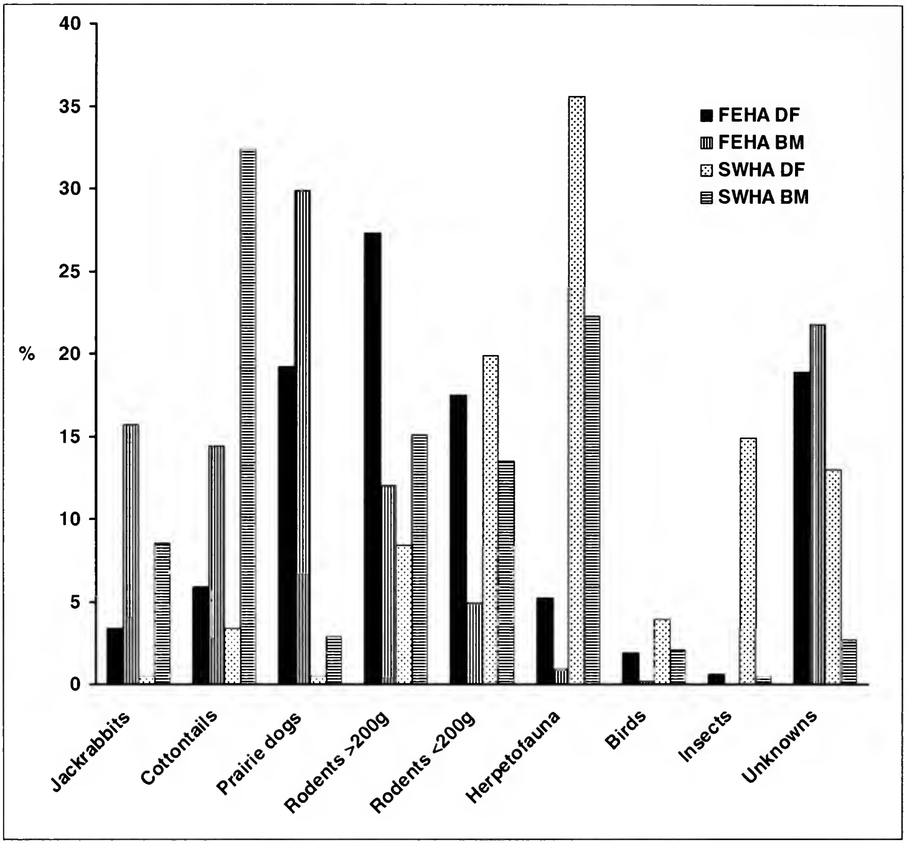

FIG. 2. Prey type delivery frequency (DF) and biomass (BM) for Ferruginous Hawk (FEHA) (n = 12) and Swainson's Hawk (SWHA) nests (n = 14) during the 2003–2004 breeding seasons.

Frequently delivered prey types included pocket gophers (25.2%), black-tailed prairie dogs (19.2%), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*; 10.3%), and cottontails (5.9%) (Fig. 2, Appendix). Black-tailed prairie dogs (29.9%), black-tailed jackrabbits (15.8%), cottontails (14.4%), and pocket gophers (10.9%) accounted for most of the prey biomass (71%) (Fig. 2, Appendix).

Swainson's Hawk Food Habits.—We video-monitored 6 Swainson's Hawks nests in 2003 and 8 different nests in 2004, and assumed all nesting pairs to be different and independent between years. We recorded 2,387 daylight hrs ($\bar{x}$ = 171 ± 25 hrs/nest) of video footage, and identified 831 of the 1,057 (79%) prey deliveries to species, genus, or family.

Frequently delivered prey types included grasshoppers (14.9%), Texas horned lizards (13.4%), Great Plains skinks (11.8%), and pocket gophers (5.9%) (Fig. 2, Appendix). Reptiles, amphibians, and insects accounted for 51% of the prey delivered by Swainson's Hawks, but small mammals accounted for 72% of the prey biomass. Important prey types in terms of biomass included cottontails (32.4%), pocket gophers (9.8%), black-tailed jackrabbits (8.5%), and bullsnakes (*Pituophis catenifer sayi*; 8.2%) (Fig. 2, Appendix).

Comparative Food Habits.—Ferruginous Hawks delivered black-tailed prairie dogs ($\bar{x}$ = 18.9 ± 5.2% per nest) more frequently than Swainson's Hawks ($\bar{x}$ = 0.5 ± 0.2% per nest; U = 236, $P < 0.001$). Ferruginous Hawks used mammalian prey of >200 g ($\bar{x}$ = 55.6 ± 3.5% per nest) more than Swainson's Hawks ($\bar{x}$ = 13.4 ± 2.7% per nest; t_{24} = 9.72, $P <$ 0.001). Swainson's Hawks delivered more grasshoppers ($\bar{x}$ = 12.7 ± 4.3% per nest vs. $\bar{x}$ = 0.4 ± 0.3% per nest; U = 24, $P < 0.001$), and reptiles and amphibians ($\bar{x}$ = 38.0 ± 5.6%

TABLE 1. Mean (± SE) deliveries/nestling/day (d/n/d) and g/nestling/day (g/n/d) for Ferruginous Hawk nests with two nestlings (n = 1), three nestlings (n = 6), and four nestlings (n = 5), and Swainson's Hawk nests with one nestling (n = 2), two nestlings[a] (n = 6), and three nestlings[b] (n = 6).

	Ferruginous Hawk		Swainson's Hawk	
Brood size	d/n/d	g/n/d	d/n/d	g/n/d
1			5.1 ± 1.7	483 ± 133
2	1.9	750	3.1 ± 0.6	466 ± 57
3	1.7 ± 0.2	694 ± 83	2.8 ± 0.2	347 ± 54
4	1.1 ± 0.1	626 ± 56		

[a] One of the six nests with two nestlings experienced a single nestling mortality; this nest was subsequently analyzed as a nest with one nestling.
[b] One of the nests with three nestlings experienced a single nestling mortality; this nest was subsequently analyzed as a nest with two nestlings.

per nest vs. $\bar{x}$ = 4.7 ± 1.2% per nest; t_{24} = 5.3, $P < 0.001$) than Ferruginous Hawks.

Most of the biomass consumed per nest by both hawk species consisted of mammals (t_{24} = 1.46, P = 0.16). Swainson's Hawks delivered more mass than Ferruginous Hawks in reptile and amphibian prey ($\bar{x}$ = 23.5 ± 4.0% per nest vs. $\bar{x}$ = 0.8 ± 0.2% per nest; U = 19, $P < 0.001$), birds ($\bar{x}$ = 2.3 ± 0.8% per nest vs. $\bar{x}$ = 0.3 ± 0.1% per nest; U = 45.0, P = 0.040), and grasshoppers ($\bar{x}$ = 0.7 ± 0.4% per nest vs. $\bar{x}$ = 0% per nest; U = 25, P = 0.008).

Ferruginous Hawks had a lower measure of diet richness per nest (10.0 ± 0.7) than Swainson's Hawks (13.4 ± 1.1; t_{24} = 2.4, P = 0.024), but diet breadth did not differ between Ferruginous (FT = 0.86) and Swainson's hawks (FT = 0.88; t_{24} = 0.88, P = 0.39). Prey overlap, on a scale of 0 to 1 with 0 indicating no dietary overlap and 1 indicating complete dietary overlap, was low in terms of prey species used (C_H = 0.31), but higher in terms of prey species' biomass contribution (C_H = 0.56).

Swainson's Hawks made more prey deliveries/day (7.0 ± 0.7 per nest) than Ferruginous Hawks (4.6 ± 0.3 per nest; U = 33.0, P = 0.008), but delivered smaller prey (147 ± 23 g/delivery) than Ferruginous Hawks (480 ± 32 g/delivery; t_{24} = 8.7, $P < 0.001$). This resulted in fewer total grams delivered/day (1,029 ± 104) at Swainson's Hawk nests compared to Ferruginous Hawk nests (2,209 ± 171; t_{24} = 6.8, $P < 0.001$). Swainson's Hawks made more prey deliveries/nestling/day (3.4 ± 0.5) than Ferruginous Hawks (1.4 ± 0.1; U = 8.0, $P < 0.001$), but delivered fewer g/nestling/day (401 ± 38) than Ferruginous Hawks (670 ± 46; t_{24} = 4.5, $P < 0.001$).

Deliveries/day did not differ among Ferruginous Hawk nests with broods of 2, 3, and 4 nestlings (H = 2.5, P = 0.28) but deliveries/nestling/day decreased with broods of 2, 3, and 4 nestlings ($F_{2,9}$ = 5.67, P = 0.025) (Table 1). Adults delivered ~500 g of additional food/day with each additional nestling, but this trend was not significant ($F_{2,9}$ = 1.7, P = 0.24) (Table 1). The provisioned g/nestling/day did not decrease with increasing brood size ($F_{2,9}$ = 0.32, P = 0.73) (Table 1), but the apparent decrease may be biologically relevant; our sample size was insufficient to reveal statistical significance.

We observed similar effects of brood size on delivery rates with Swainson's Hawks. Prey deliveries/day among Swainson's Hawk nests tended to increase with increasing brood sizes but differences were not significant ($F_{2,13}$ = 2.4, P = 0.13). An apparent decrease in deliveries/nestling/day with increasing brood size was not significant (H = 3.99, P = 0.14) (Table 1). There appeared to be an increase in delivered g/day as brood size increased, but differences were not significant ($F_{2,9}$ = 1.7, P = 0.24). Ultimately, provisioned g/nestling/day did not differ among brood sizes ($F_{2,13}$ = 0.62, P = 0.55) (Table 1).

Provisioning rates of Ferruginous Hawks did not vary with 5-day nestling growth intervals in terms of delivered g/hr ($F_{8,49}$ = 0.58, P = 0.79) or g/nestling/hr ($F_{8,49}$ = 0.78, P = 0.62) (Table 2). Similarly, Swainson's Hawk prey provisioning rates did not vary with 5-day nestling growth intervals in terms of delivered g/hr ($F_{7,40}$ = 1.58, P = 0.17) or g/nestling/hr ($F_{7,40}$ = 0.59, P = 0.76) (Table 2).

DISCUSSION

Different life history traits (e.g., migratory behavior, morphology, and clutch size) may

TABLE 2. Prey deliveries/hr (d/hr), deliveries/nestling/hr (d/n/hr), g/hr, and g/nestling/hr (g/n/hr) ($\bar{x} \pm$ SE) for Ferruginous Hawk (FEHA) ($n = 12$) and Swainson's Hawk (SWHA) nests ($n = 14$) during 5-day age intervals of the nestling development period.

	Age (days)								
	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50
Prey deliveries/hr									
FEHA	0.26 ± 0.04	0.29 ± 0.04	0.38 ± 0.06	0.36 ± 0.03	0.34 ± 0.04	0.29 ± 0.02	0.32 ± 0.03	0.26 ± 0.01	0.22 ± 0.02
SWHA	0.35	0.36 ± 0.04	0.46 ± 0.17	0.45 ± 0.07	0.57 ± 0.07	0.48 ± 0.07	0.40 ± 0.04	0.44 ± 0.06	—
Deliveries/nestling/hr									
FEHA	0.08 ± 0.01	0.10 ± 0.01	0.13 ± 0.02	0.12 ± 0.01	0.10 ± 0.01	0.09 ± 0.01	0.10 ± 0.01	0.08 ± 0.01	0.07 ± 0.01
SWHA	0.35	0.31 ± 0.08	0.40 ± 0.19	0.26 ± 0.05	0.30 ± 0.05	0.22 ± 0.03	0.24 ± 0.05	0.24 ± 0.05	—
Grams/hr									
FEHA	129 ± 25	137 ± 8	168 ± 36	176 ± 27	173 ± 21	138 ± 14	172 ± 31	144 ± 10	144 ± 35
SWHA	25	27 ± 5	31 ± 10	36 ± 7	61 ± 11	66 ± 12	76 ± 14	52 ± 14	—
Grams/nestling/hr									
FEHA	39 ± 7	46 ± 3	56 ± 12	57 ± 9	53 ± 8	43 ± 4	52 ± 7	42 ± 3	48 ± 12
SWHA	25	21 ± 2	26 ± 11	22 ± 7	33 ± 7	31 ± 5	45 ± 14	25 ± 6	—

have varying effects on prey use and potential resource partitioning between Ferruginous and Swainson's hawks. Earlier diet studies of sympatric Ferruginous and Swainson's hawks indicated high diet overlap (82–98%) despite behavioral and morphological differences (Schmutz et al. 1980, Restani 1991). Ferruginous and Swainson's hawks in our study displayed low prey use overlap (31%) which may be geographically and/or temporally unique. It is also possible that lower diet overlap is more common in other sympatric populations, but only detectable with more accurate data obtained by nest video monitoring rather than analysis of pellet and prey remains (Simmons et al. 1991, Lewis 2001). Low interspecific dietary overlap and high dietary breadth could indicate high prey availability and low interspecific dietary competition. However, confirmation requires estimates of prey densities across breeding seasons (Schmutz and Hungle 1989, Woffinden and Murphy 1989).

A few relatively larger mammalian prey species dominated prey delivery frequency and percentage biomass delivered by Ferruginous Hawks in our study population. Breeding Ferruginous Hawks preyed primarily upon black-tailed jackrabbits in Utah (Woffinden and Murphy 1977), northern pocket gophers (*Thomomys talpoides*) and ground squirrels in Idaho (Wakeley 1978, Steenhof and Kochert 1985), Richardson's ground squirrels (*Spermophilus richardsoni*) in North Dakota (Gilmer and Stewart 1983), Wyoming (MacLaren et al. 1988), and Alberta (Schmutz et al. 1980), and *Spermophilus* ground squirrels in Montana (Restani 1991). Prairie dog species are the main prey resource for wintering Ferruginous Hawks (Schmutz and Fyfe 1987, Cully 1991, Plumpton and Andersen 1997). Gunnison's prairie dog (*Cynomys gunnisoni*) was reported as a primary breeding season prey resource in New Mexico (Cartron et al. 2004), but the diet percentage was derived from pellet and prey remains. Indirect methods of diet analysis (i.e., analysis of pellets and remains) are known to bias results toward species whose remains are more detectable (e.g., large bones, thick skin, bright feathers) (Collopy 1983, Simmons et al. 1991, Bielefeldt et al. 1992), but Cartron et al.'s (2004) data still indicate the regular use of prairie dogs by breeding Ferruginous Hawks. The finer resolution of our data indicate black-tailed prairie dogs were the second most frequently delivered prey item to Ferruginous Hawk nests and contributed the most biomass. Thus, we believe that black-tailed prairie dogs are a substantial, if not critical, prey resource for breeding Ferruginous Hawks in the Southern Great Plains.

Previous diet assessments for breeding Swainson's Hawks vary widely across their range but were dominated by *Spermophilus* ground squirrels, small rodents, and birds in Alberta (95.3%; Schmutz et al. 1980), California (82.6%; Woodbridge 1987), North Dakota (100%; Gilmer and Stewart 1984), Saskatchewan (95.6%; England et al. 1997), and Washington (50%; Fitzner 1980). In Washington, however, reptiles (32%) and insects (12%) were also important prey resources (Fitzner 1980). Swainson's Hawks in Utah preyed primarily upon *Lepus* and *Sylvilagus* rabbits (56.1%) but also insects (19.5%), small rodents (12.2%), and birds (9.7%) (Smith and Murphy 1973). Reptiles (42.2%) dominated the Swainson's Hawk diet in Arizona (Porton 1977), and insects (54.9%) dominated in New Mexico (Bednarz 1988). The breeding Swainson's Hawks we monitored delivered primarily reptiles and amphibians (35.6%), rodents (28.7%), and grasshoppers (14.9%). This large variability among diets confirms the opportunistic ability of Swainson's Hawks to use a diversity of prey types across their range.

Breeding adults apparently compensate for the extra caloric demand of larger broods by foraging more often and/or further from the nest, and selecting different types and sizes of prey (Wright et al. 1998). Peregrine Falcons (*Falco peregrinus*) in Alaska (Palmer et al. 2004) and Northern Goshawks (*Accipiter gentilis*) in Minnesota (Smithers et al. 2005) increased prey delivery rates and prey size with larger broods, but deliveries/nestling still decreased. Similarly, Masman et al. (1988) showed that Eurasian Kestrels (*Falco tinnunculus*) responded to experimentally increased brood sizes by increasing foraging efforts and food delivery rates, and changing food type and size.

Prey size, deliveries/day, g/day, and deliveries and g/nestling/day did not vary significantly for Ferruginous Hawk nests with different brood sizes in our study area. However, sample sizes for both hawk species may have been too low to detect statistical relationships between prey delivery rates and brood sizes at an *alpha* level of 0.05. Ferruginous Hawks delivered ~500 g of additional food/day with each additional nestling increase in brood size, and this trend is probably biologically significant. Nestling provisioning rates in g/nestling/day, however, decreased with increasing brood size. Thus, Ferruginous Hawks delivered more g/day with increasing brood size but did not maintain a constant nestling provisioning rate.

Our results are similar to those of Palmer et al. (2004) and Smithers et al. (2005) in that Ferruginous and Swainson's hawks increased prey deliveries and mass/day, but did not compensate sufficiently with increased delivery frequency or larger prey items to maintain consistent g/nestling/day with increasing brood sizes. This suggests that single nestlings may receive an abundance of food while nestlings in larger broods may receive the necessary caloric requirements but experience comparatively slower growth rates and poorer physiological condition at fledging (Olendorff 1974, Wakeley 1978).

Prey delivery and nestling provisioning rates, and caloric requirements also can vary across the nestling growth period. Olendorff (1974) found that food consumption of captive Ferruginous Hawk nestlings peaked at post-hatch week 4 (days 22–28) and food consumption of Swainson's Hawk nestlings peaked at post-hatch week 5 (days 29–35). Our results approximate these findings as Ferruginous Hawks delivered the most g/nestling/hr during post-hatch days 21–25, and Swainson's Hawks delivered the most g/nestling/hr during post-hatch days 36–40.

Prey use overlap was low between breeding Ferruginous and Swainson's hawks, but overlap in terms of prey contributing the most biomass was higher. This may be explained by Swainson's Hawks taking fewer of the large prey types used frequently by Ferruginous Hawks, and those prey contributing disproportionately more biomass to the diet. We suspect consistent deliveries of small prey, compared to irregular or occasional deliveries of large prey, is of equal or more importance for breeding Swainson's Hawks (e.g., consistent provisioning of metabolic water; Kirkley and Gessaman 1990).

Ferruginous Hawks preyed primarily upon prairie dogs and pocket gophers. These species should be considered when making management decisions for breeding and non-breeding Ferruginous Hawks on the Southern Great Plains. Numerous studies have shown that Ferruginous Hawks tend to have lower reproductive success and emigrate following primary prey population declines (Smith et al. 1981, Schmutz and Hungle 1989, Woffinden and Murphy 1989, Cully 1991). These trends may be particularly important where prairie dogs are a primary breeding or non-breeding season prey species, as they are still subject to unregulated eradication and control efforts throughout most of their range (Kotliar et al. 1999).

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APPENDIX. Prey delivery frequency (DF) and biomass (BM) at Ferruginous Hawk (n = 12) and Swainson's Hawk nests (n = 14) during the 2003–2004 breeding seasons.

	Ferruginous Hawk			Swainson's Hawk		
Prey type	*n*	% DF	% BM	*n*	% DF	% BM
Rodentia						
Pocket gopher spp. (*Geomys bursarius*) (*Cratogeomys castanops*)	236	25.2	10.9	62	5.9	9.8
Black-tailed prairie dog (*Cynomys ludovicianus*)	180	19.2	29.9	5	0.5	2.9
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	96	10.3	3.8	35	3.3	4.8
Southern plains woodrat (*Neotoma micropus*)	20	2.1	1.1	26	2.5	4.9
Spotted ground squirrel (*Spermophilus spilosoma*)	20	2.1	0.5	10	0.9	0.8
Ord's kangaroo rat (*Dipodomys ordii*)	19	2.0	0.3	35	3.3	1.9
Northern grasshopper mouse (*Onychomys leucogaster*)	6	0.6	<0.1	21	2.0	0.6
Deer mouse (*Peromyscus maniculatus*)	6	0.6	<0.1	43	4.1	0.8
Hispid cotton rat (*Sigmodon hispidus*)	1	0.1	<0.1	28	2.6	3.8
Hispid pocket mouse (*Chaetodipus hispidus*)	0	0.0	0.0	14	1.3	0.4
Plains pocket/harvest mouse (*Perognathus flavescens*) (*Reithrodontomys montanus*)	0	0.0	0.0	10	0.9	0.1
House mouse (*Mus musculus*)	0	0.0	0.0	4	0.4	0.1
Norway rat (*Rattus norvegicus*)	0	0.0	0.0	1	0.9	0.4
Unknown rodent spp.	16	1.7	0.2	10	0.1	0.3
Totals	600	63.9	47.0	304	28.7	31.6
Lagomorpha						
Cottontail spp. (*Sylvilagus floridanus*) (*S. audubonii*)	55	5.9	14.4	36	3.4	32.4
Black-tailed jackrabbit (*Lepus californicus*)	32	3.4	15.7	5	0.5	8.5
Totals	87	9.3	30.1	41	3.9	40.9
Reptilia and Amphibia						
Texas horned lizard (*Phrynosoma cornutum*)	23	2.5	0.2	131	12.4	3.0
Eastern yellow-bellied racer (*Coluber constrictor flaviventris*)	4	0.4	0.1	30	2.8	2.5
Bullsnake (*Pituophis catenifer sayi*)	3	0.3	0.3	28	2.6	8.2
Great Plains skink (*Eumeces obsoletus*)	2	0.2	<0.1	125	11.8	2.4
Western coachwhip (*Masticophus flagellum testaceus*)	1	0.1	0.1	12	1.1	3.6
Western Plains garter snake (*Thamnophis radix haydeni*)	1	0.1	<0.1	0	0.0	0.0
Plains hognose (*Heterodon nasicus nasicus*)	0	0.0	0.0	6	0.6	0.7
Central Plains milk snake (*Lampropeltis triangulum gentiles*)	0	0.0	0.0	2	0.2	0.1
Ground snake (*Sonora semiannulata*)	0	0.0	0.0	1	0.1	<0.1
Unknown frog/toad spp.	9	1.0	<0.1	13	1.2	0.2
Unknown snake spp.	6	0.6	0.2	10	0.9	1.4
Unknown lizard spp.	0	0.0	0.0	20	1.9	0.2
Totals	49	5.2	0.9	378	35.6	22.3

APPENDIX. Continued.

	Ferruginous Hawk			Swainson's Hawk		
Prey type	*n*	% DF	% BM	*n*	% DF	% BM
Aves						
Burrowing Owl (*Athene cunicularia*)	3	0.3	0.1	0	0.0	0.0
Western Meadowlark (*Sturnella neglecta*)	2	0.2	<0.1	6	0.6	0.4
Common Nighthawk (*Chordeiles minor*)	1	0.1	<0.1	0	0.0	0.0
Lark Bunting (*Calamospiza melanocorys*)	1	0.1	0.0[a]	1	0.1	<0.1
Scaled Quail (*Callipepla squamata*)	0	0.0	0.0	3	0.3	0.4
European Starling (*Sturnus vulgaris*)	0	0.0	0.0	1	0.1	0.1
Killdeer (*Charadrius vociferous*)	0	0.0	0.0	1	0.1	0.1
Loggerhead Shrike (*Lanius ludovicianus*)	0	0.0	0.0	1	0.1	<0.1
Unknown bird	11	1.2	0.1	27	2.6	1.1
Totals	18	1.9	0.2	40	3.9	2.1
Insecta						
Grasshopper spp. (*Brachystola magna*)	6	0.6	<0.1	157	14.9	0.5
Unknown	177	18.9	21.8	137	13.0	2.7
Totals	937			1057		

[a] Prey item flew away after delivery.

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NESTING HABITAT RELATIONSHIPS OF SYMPATRIC CRESTED CARACARAS, RED-TAILED HAWKS, AND WHITE-TAILED HAWKS IN SOUTH TEXAS

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ABSTRACT.—We quantified nesting-site habitats for sympatric White-tailed Hawks (*Buteo albicaudatus*) (*n* = 40), Red-tailed Hawks (*B. jamaicensis*) (*n* = 39), and Crested Caracaras (*Caracara cheriway*) (*n* = 24) in the Coastal Sand Plain of south Texas. White-tailed Hawks and Crested Caracara nest sites occurred in savannas, whereas Red-tailed Hawk nest sites occurred in woodlands on the edge of savannas. White-tailed Hawk nest sites were in shrubs and trees that were shorter (3.5 ± 1.0 m) and had smaller canopy diameters (5.5 ± 2.1 m) than those of Red-tailed Hawks (10.1 ± 2.0 m, 13.7 ± 5.8 m) and Crested Caracaras (5.6 ± 1.7 m, 8.5 ± 3.5 m). Red-tailed Hawk nest sites had higher woody densities (15.7 ± 9.6 plants) and more woody cover (84 ± 19%) than those of White-tailed Hawks (5.6 ± 5.8 plants, 20 ± 21%) and Crested Caracaras (9.9 ± 6.7 plants, 55 ± 34%). Crested Caracara nest sites were in dense, multi-branched shrubs composed of more living material (97 ± 3%) than those of White-tailed (88 ± 18%) and Red-tailed hawks (88 ± 18%). Nest sites of White-tailed Hawks, Red-tailed Hawks, and Crested Caracaras were similar to random samples from the surrounding habitat indicating that preferred nesting habitat was available for each of these species at least within 60 m of active nest sites. Nest tree height, along with woody plant and native grass cover best discriminated nest sites among the three raptor species. There was no overlap at Red-tailed and White-tailed hawk nest sites in vegetation structure, while Crested Caracara nests were in habitat intermediate between the two other species. Partitioning of nesting habitat may be how these raptor species co-exist at the broader landscape scale of our study area in the Coastal Sand Plain of Texas. *Received 5 July 2006. Accepted 20 February 2007.*

Nest-site selection is an important aspect of avian reproductive ecology because it reflects the environment in which adults, eggs, and nestlings will be exposed during critical periods (Travaini et al. 1994). Availability of adequate nesting habitat directly influences nesting success, productivity and, thereby, local population sizes (Newton 1979). Nest-site selection is an active process in which different species respond to stimuli based on a complex of environmental variables (Fretwell 1972). How a breeding pair or a population responds to these stimuli may impact breeding success and fitness of that pair or population. These stimuli are proximate factors that birds use to select their nesting habitat (James 1971) and may include: tree size and form, canopy height and structure, understory height, and structure and density of surrounding vegetation. The structural configuration of the nest tree has been suggested to be the most important stimulating factor for nesting raptors (Horn 1971, Titus and Mosher 1987).

Ultimate factors that affect nesting success and fitness for individual pairs, populations, or species include: proximity of foraging habitat, protection of nest and young, thermal environment of nests, and spatial interactions within the community (Smith and Murphy 1982). Proximate and ultimate factors of nest-site selection may work independently, hierarchically as a system of sequential decisions, or synergistically in a complex fashion of "niche-gestalt" (Lack 1937).

The Coastal Sand Plain (CSP) of southern Texas is inhabited year-round by breeding populations of Red-tailed Hawks (*Buteo jamaicensis*), White-tailed Hawks (*B. albicaudatus*), and Crested Caracaras (*Caracara cheriway*). These similar-sized raptors have similar breeding chronologies (Actkinson 2006), but it is unknown how they partition nesting habitat where they are sympatric. Little is known of Red-tailed Hawk habitat requirements in the CSP, and the White-tailed Hawk and Crested Caracara are two of the least scientifically understood raptors in North America (Farquhar 1992, Morrison 1996).

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Our objectives were to examine nesting habitat characteristics and partitioning of nest sites based on those characteristics among these three sympatric raptors.

STUDY AREA

This study was conducted between February and July during 2003 and 2004 on the Encino Division of the King Ranch in Brooks County, Texas (26° 56′ N, 98° 07′ W) during the breeding and nesting seasons of Red-tailed Hawks, White-tailed Hawks, and Crested Caracaras in south Texas (Actkinson 2006). The 45,000-ha area is within the CSP, which is part of the Tamaulipan biotic province (Dice 1943, Blair 1950). The area contained three distinct habitat types: mesquite (*Prosopis glandulosa*) savannah, Tamaulipan thornscrub, and live oak (*Quercus virginianus*) woodland (Lehmann 1969, Beasom 1970, Everitt et al. 1999). The mesquite savannah is open landscape of native grass-forb prairie communities interspersed with small mesquite-thornscrub mottes. The Tamaulipan thornscrub habitat is mesquite savannah moderately to heavily (≥40%) invaded by woody thornscrub. The live oak woodlands vary in structure from small (3 m tall) to large trees (≤15 m in height) with relatively open to completely closed canopies. The understory vegetation was dominated by a combination of herbaceous or woody species. The live oak woodlands occurred in open savannahs and in mixed brush areas; they provide unique habitat structure not found throughout most of south Texas. Several exotic grasses including buffelgrass (*Cenchrus ciliaris*), bermudagrass (*Cynodon dactylon*), and King Ranch bluestem (*Bothriochloa ischaemum*) have become established on a few sites in the study area. Soils were dominated by deep sands, but also included fine sandy loams and sandy clay loams (Beasom 1970).

The climate ranges from semi-arid to subtropical with mild winters and hot, humid summers (Gould 1975, Everitt et al. 1999). Average annual rainfall is 62 cm and the average length of the growing season is 240 days (Lehmann 1984). Above-average rainfall at the study area began in 2002, ending a long-term drought and continued through the entire study.

METHODS

Nest-site Measurements.—We measured nest-site characteristics about 2 weeks after young had fledged or about 4 weeks after nest failure. We identified the species for each nest tree and measured the height (highest point), canopy diameter (widest point of entire tree), and estimated the percent of the tree/shrub that was alive. We used canopy diameter rather than trunk diameter at breast height because many of the nests were in shrubs or multi-stemmed trees. We measured the horizontal cover and height of vegetation types at nest sites and within nest areas. We centered a 12-m circular plot (0.04 ha) on the nest (James and Schugart 1970) to describe the characteristics of the specific nest site (proximal site). We centered a 60-m circular plot (1.1 ha) on the nest to examine the characteristics of broader nest area (distal site).

We used a 0.5-m^2 frame at proximal nest sites to measure the percentage of native grass, exotic grass, forb, woody plant, and bare ground cover at five randomly-selected locations. Data from these five locations were averaged to obtain a mean value for each plant group at each proximal nest site. We averaged the height of all woody species ≥1 m tall and recorded the number of each species present to characterize vertical cover and composition of woody vegetation at the proximal nest site.

We used line-intercept (Canfield 1941) to measure native grass, exotic grass, forb, woody plant, and bare ground horizontal cover at the distal nest site scale along four 60-m transects extending from the nest tree, separated by 90° and oriented from a randomly-selected compass bearing. We calculated the average of each of the five plant groups from the four transects and divided the average by transect length to estimate percent cover of each group. We used a pole marked with alternating light and dark decimeters to measure height of vegetation at four different distances (15, 30, 45, 60 m) from the nest along each transect following Robel et al. (1970). Vegetation heights obtained from each transect were averaged to provide a mean cover height for each distance.

Paired sites were randomly selected for each raptor nest site to characterize habitat that was available to nesting raptors and were measured using the same sampling techniques. This was done to examine how each species used habitat in relation to that available as opposed to how they used habitat in relation to each other. Locations of paired, random sites were chosen from a randomly-selected bearing (0–360°) and distance (120–500 m) from the raptor nest. A minimum distance of 120 m was necessary to prevent overlap of the 60-m transects. The maximum distance of 500 m was chosen so that paired, random nest sites were within the home ranges of nesting birds, which increased the probability that a random nest site reflected habitat available to nesting birds. The closest tree to a randomly-selected point that was at least as tall as the lowest recorded nest tree height for each respective species and capable of supporting a nest (Smith et al. 2003) was selected as the center point of the paired, random site.

Statistical Analysis.—We analyzed differences and correlation values of nest-site variables to avoid redundant variables and to obtain the most parsimonious model that adequately discriminated the associated groups representing each raptor species and/or paired random plots (Green 1979). We used one-way analysis of variance (ANOVA) to analyze differences in variables among the three species. We compared raptor nest sites to paired, random sites (Conner et al. 1983) with a two-tailed Student's t-test (Sokal and Rohlf 1981) to assess nest-site features used by each species in relation to available habitat. Variables with a difference ($P \geq 0.05$) among groups were excluded from the three-group discriminant function analysis (DFA) (Cooley and Lohnes 1971) but not the two-group DFA. The three-group DFA was used to examine how each species used nesting habitat in relation to each other. An *alpha* level of ($P < 0.01$) was used for the two-group DFA to differentiate between variables at nest sites and random sites. This provided an opportunity to use two-group DFA to derive linear combinations of selected variables to identify potential differences between nest sites and comparable randomly located sites. Highly correlated ($r \geq 0.60$) variables were removed from analyses. Nest tree and habitat variables were used in a DFA with forward stepwise inclusion of variables (Cody 1968, James 1971) to compare the respective nest sites of Red-tailed Hawks, White-tailed Hawks, and Crested Caracaras. Stepwise analysis in each DFA was used to statistically classify nest sites as one of the three raptor species (three-group DFA) or as a random sample (two-group DFA). All statistical procedures were conducted using Statistica (2004) software. All data are presented as means ± SD.

RESULTS

Nest-site Descriptions.—We described nesting habitat characteristics at 40 White-tailed Hawk, 39 Red-tailed Hawk, and 24 Crested Caracara nests. White-tailed Hawk nest sites were primarily within savannahs dominated by native grasses and forbs interspersed with scattered mottes of shrubs and trees. White-tailed Hawks tended to use shrubs and trees that were shorter (TREEHT: < 3.5 ± 1.0 m) and had smaller canopy diameters (CANOPYDIA: <5.5 ± 2.1 m) than at Red-tailed Hawk (TREEHT: <10.1 ± 2.0 m, CANOPYDIA: <13.7 ± 5.8 m) and Crested Caracara nest sites (TREEHT: <5.6 ± 1.7 m, CANOPYDIA: <8.5 ± 3.5 m) (Table 1).

White-tailed Hawk nests occurred in nine woody species. Most nest substrates were in thorny evergreen shrubs, including granjeno (*Celtis pallida*) ($n = 14$) followed by mesquite ($n = 12$), lime prickly ash (*Zanthoxylum fagara*) ($n = 5$), brasil (*Condalia hookeri*) ($n = 5$), Texas ebony (*Pithecellobium ebano*) ($n = 2$), huisache (*Acacia farnesiana*) ($n = 1$), and all thorn (*Koeberlinia spinosa*) ($n = 1$). White-tailed Hawk nests were built within or near the crowns of these substrates and most were exposed to direct sunlight but concealed laterally by vines and dense branches. Nests in more sparsely-branched mesquite trees were generally in forks between major branches and were often only partially concealed.

Proximal nest sites of White-tailed Hawks were characterized by higher percentages of native grass (NATGR1: 46 ± 24%) and bare ground (BARGND1: 10 ± 9%), lower percentages of woody cover (WOODY1: 20 ± 21%), and fewer woody plants (WOODDEN: 5.6 ± 5.8) that were shorter in height (WOODHT: 2.1 ± 1.3 m) than Red-tailed Hawk and Crested Caracara nest sites (Table 1). The same trends were apparent at distal nest sites relative to vegetative cover types at

TABLE 1. Variables at White-tailed Hawk (WTHA) (n = 40), Red-tailed Hawk (RTHA) (n = 39), and Crested Caracara (CRCA) (n = 24) nest sites in Brooks County, Texas, 2003–2004.

	WTHA	RTHA	CRCA		
Variable[a]	$\bar{x} \pm$ SD	$\bar{x} \pm$ SD	$\bar{x} \pm$ SD	P	F[b]
NATGR1	46 ± 24	5 ± 9	16 ± 16	< 0.001	55.65
EXOTGR1	1 ± 6	2 ± 8	1 ± 3	> 0.05	0.25
FORB1	23 ± 17	8 ± 11	26 ± 22	< 0.001	12.95
WOODY1	20 ± 21	84 ± 19	55 ± 34	< 0.001	70.59
BARGND1	10 ± 9	2 ± 4	3 ± 4	< 0.001	17.34
WOODDEN	5.6 ± 5.8	15.7 ± 9.6	9.9 ± 6.7	< 0.001	17.24
WOODHT	2.1 ± 1.3	5.8 ± 1.7	3.5 ± 1.8	< 0.001	58.25
TREEHT	3.5 ± 1.0	10.1 ± 2.0	5.6 ± 1.7	< 0.001	167.36
CANOPYDIA	5.5 ± 2.1	13.7 ± 5.8	8.5 ± 3.5	< 0.001	40.11
TREEALV	88 ± 18	88 ± 17	97 ± 3	$0.025 < P < 0.05$	3.26
NATGR2	60 ± 16	23 ± 14	38 ± 22	< 0.001	49.20
EXOTGR2	0 ± 1	3 ± 9	1 ± 4	> 0.05	1.87
FORB2	24 ± 13	22 ± 12	28 ± 17	> 0.05	1.59
WOODY2	9 ± 5	47 ± 16	28 ± 25	< 0.001	60.10
BARGND2	7 ± 5	5 ± 4	5 ± 4	> 0.05	2.14
15VERTHT	0.5 ± 0.3	4.3 ± 2.5	1.7 ± 2.1	< 0.001	41.78
30VERTHT	0.5 ± 0.3	2.4 ± 1.8	1.4 ± 1.7	< 0.001	17.40
45VERTHT	0.5 ± 0.3	1.9 ± 1.6	1.2 ± 1.4	< 0.001	13.82
60VERTHT	0.7 ± 0.5	2.3 ± 1.7	1.4 ± 1.3	< 0.001	16.12

[a] 1 = 12-m radius, 2 = 60-m radius. NATGR1 = percent of native grass cover, EXOTGR1 = percent of exotic grass cover, FORB1 = percent of forb cover, WOODY1 = percent of woody cover, BARGND1 = percent of bare ground, WOODDEN1 = number of woody plants ≥ 1 m tall, WOODHT1 = height of woody plants ≥ 1 m, TREEHT = height of nest tree (m), CANOPYDIA = canopy diameter of the nest tree (m), TREEALV = percent of nest tree alive, NATGR2 = percent of native grass cover, EXOTGR2 = percent of exotic grass cover, FORB2 = percent of forb cover, WOODY2 = percent of woody cover, BARGND2 = percent of bare ground, 15VERTHT = mean vertical cover height 15 m from nest, 30VERTHT = mean vertical cover height 30 m from nest, 45VERTHT = mean vertical cover height 45 m from nest, and 60VERTHT = mean vertical cover height 60 m from nest.

[b] One-way ANOVA (df = 2, 100) comparing variable means of three raptor species.

proximal nest sites (Table 1). Vertical cover heights measured at 15 m (15VERTHT: 0.5 ± 0.3 m), 30 m (30VERTHT: 0.5 ± 0.3 m), 45 m (45VERTHT: 0.5 ± 0.3 m), and 60 m (60VERTHT: 0.7 ± 0.5 m) from the nest were lower than those measured for Red-tailed Hawks and Crested Caracara.

Red-tailed Hawk nest sites were within live oak woodlands and mesquite-dominated tree lines adjacent to open savannah habitats, and were in live oak (n = 27) and mesquite (n = 12) trees. Red-tailed Hawk nests were in trees that were taller (TREEHT: 10.1 ± 2.0 m) and had larger canopy diameters (CANOPYDIA: 13.7 ± 5.8 m) than nest substrates used by White-tailed Hawks and Crested Caracaras (Table 1). Nests were often concealed by dense canopies of live oaks. Mistletoe (*Phoradendron* spp.) provided additional nest concealment in some mesquite trees and was used as a support for nests. Proximal nest sites of Red-tailed Hawks had taller woody plant heights (WOODHT: 5.8 ± 1.7 m), higher percentages of woody cover (WOODY1: 84 ± 19%) and number of woody plants (WOODDEN: 15.7 ± 9.6), and lower percentages of native grass (NATGR1: 5 ± 9%), forbs (FORB1: 8 ± 11%), and bare ground (BARGND1: 2 ± 4%) (Table 1). Vertical cover heights at 15 m (15VERTHT: 4.3 ± 2.5 m), 30 m (30VERTHT: 2.4 ± 1.8 m), 45 m (45VERTHT: 1.9 ± 1.6 m), and 60 m (60VERTHT: 2.3 ± 1.7 m) from the nest were higher than for White-tailed Hawks and Crested Caracaras.

Crested Caracara nest sites were similar to those of White-tailed Hawks as they were primarily within savannas, but were in slightly taller (TREEHT: 5.6 ± 1.7 m) substrates with larger canopy diameters (CANOPYDIA: 8.5 ± 3.5 m) (Table 1). Crested Caracaras preferred densely-branched, thorny trees and shrubs (e.g., granjeno), although they usually constructed their nests within the interior of these substrates at heights similar to White-tailed Hawk nests. Most Crested Caracara nests occurred in granjeno (n = 15), followed by all thorn (n = 5), mesquite (n = 2), huisache (n = 1), and Texas persimmon (*Diospyros texana*) (n = 1). Nest substrates typi-

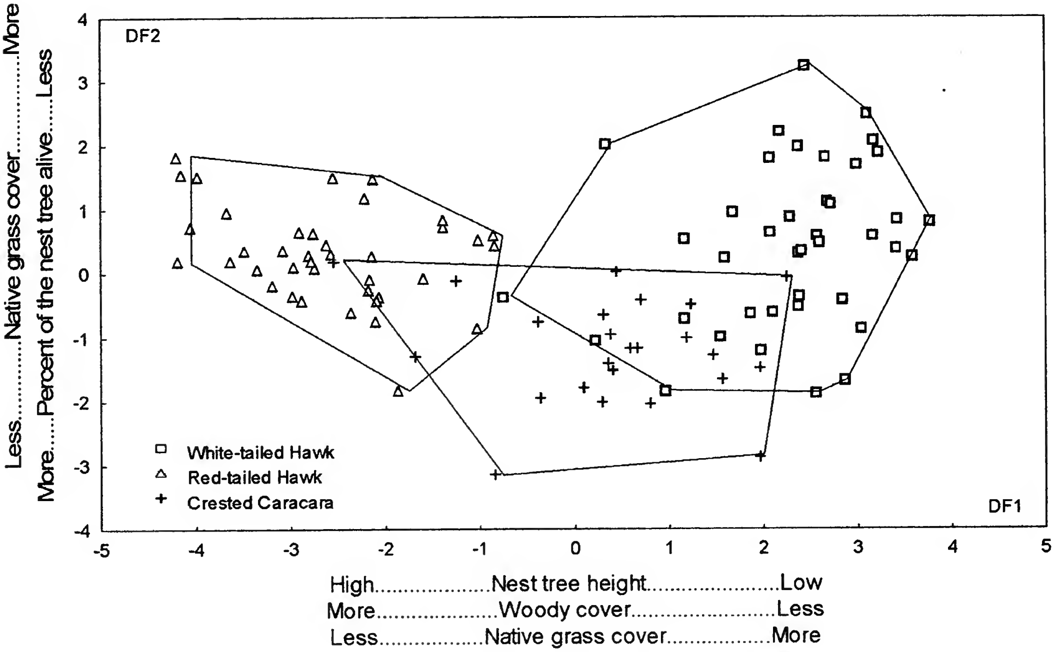

FIG. 1. Variation in nest trees and habitat composition at White-tailed Hawk, Red-tailed Hawk, and Crested Caracara nest sites in Brooks County, Texas based on a three-group discriminant function analysis. Each symbol represents a raptor nest site.

cally had more living material (TREEALV: 97 ± 3%) than either White-tailed or Red-tailed hawk nests. Proximal nest sites of the Crested Caracara contained higher percentages of forb cover (FORB1: 26 ± 22%) than the other two species. Distal nest sites of Crested Caracaras consisted of higher percentages of native grass cover (NATGR2: 38 ± 22%) than Red-tailed Hawk, but less than White-tailed Hawk nest sites. The percentage of woody cover was higher in Crested Caracara distal nest sites (WOODY2: 28 ± 25%) than at White-tailed Hawk nest sites, but lower than at Red-tailed Hawk nest sites. Vertical cover heights at 15 m (15VERTHT: 1.7 ± 2.1 m), 30 m (30VERTHT: 1.4 ± 1.7 m), 45 m (45VERTHT: 1.2 ± 1.4 m), and 60 m (60VERTHT: 4 ± 1.3 m) at Crested Caracara nests were higher than those at White-tailed Hawk nests but lower than those of Red-tailed Hawk nests.

Multivariate Comparisons of Nest Sites Among Species.—Fifteen variables differed ($P \leq 0.05$) among the nest sites of the three hawk species (Table 1). Stepwise analysis of the three-group DFA identified three variables that best discriminated nest sites of the three species. Nest sites were best discriminated by nest tree height, native grass cover, and horizontal woody plant cover along DF1 (eigenvalue = 4.72, Wilks' lambda = 0.12, $P \leq 0.001$), (Fig. 1). Nest sites were best discriminated along DF2 (eigenvalue = 0.466, Wilks' lambda = 0.682, $P \leq 0.001$) by the percentage of the nest tree that was alive and native grass cover. Complete separation of nest sites was apparent between White-tailed and Red-tailed hawks, whereas Crested Caracara nest sites shared characteristics with those of the other two species (Table 1, Fig. 1).

The overall correct classification of each species' nest sites was high (89% compared to the 33% prior probability of correct classification); within species, 88% of White-tailed Hawk, 97% of Red-tailed Hawk, and 79% of Crested Caracara nest sites were correctly classified (Table 2). None of the White-tailed or Red-tailed hawk nests sites was incorrectly classified as the other species, indicating they used distinctly different nest sites. Nest tree height was shorter, there was more native grass cover and less woody cover in

TABLE 2. Three-group discriminant function analysis of nest-site features of White-tailed Hawk (WTHA), Red-tailed Hawk (RTHA), and Crested Caracara (CRCA) nest sites in Brooks County, Texas, 2003–2004.

			Predicted number of nests		
Species	*n*	Correct (%)	WTHA	RTHA	CRCA
WTHA	40	88	35	0	5
RTHA	39	97	0	38	1
CRCA	24	79	2	3	19
Totals	103	89	37	41	25

White-tailed Hawk nesting habitat than in Red-tailed Hawk nesting habitat (Fig. 1).

Nest Sites versus Random Sites.—Comparisons of nest sites and randomly sampled sites at proximal and distal sampling locations revealed no significant differences between nest-sites and random sites at an *alpha* level < 0.05 (Table 3). However, four nest-site variables differed for each species at an *alpha* level of < 0.1. This provided an opportunity to use two-group DFA to derive linear combinations of these variables to identify potential differences between nest sites of each species with a comparable sample of randomly located sites. This permitted us to show how each species used nesting habitat in relation to that available. We identified significant ($P < 0.005$) and biologically meaningful relationships from the linear combinations of the variables (Table 3) in all comparisons of nest and random sites for all three species.

Four nest-site variables differed ($P \leq 0.01$) between White-tailed Hawk nests and paired random sites (Table 3). White-tailed Hawk nest sites had smaller nest substrates with more dead material, less distal woody cover, and lower plant heights 15 m from the nest than random sites. The DF (eigenvalue = 0.204, Wilks' lambda = 0.831, $P = 0.003$) was a function of decreasing nest tree canopy diameter, vegetation height 15 m from the nest, and percent of the nest tree that was alive. Classification of nest sites and paired sites into their correct group was 78% for White-tailed Hawk nest sites and 62% for paired sites, giving an overall correct classification of 70%, which was 20% greater than the 50% prior probability of classification. We did not achieve "perfect" classification success (100%), but an overall 70% classification rate indicates the DFA models were about 20% greater than random with a 30% overlap between White-tailed Hawk nesting habitat components in relation to what was available.

Four nest-site variables differed ($P \leq 0.10$) between Red-tailed Hawk nest sites and paired, random sites (Table 3). Red-tailed Hawk nest sites had less native grass cover, more woody plants that were taller, and taller nest trees compared to the paired sites. The DF (eigenvalue = 0.27, Wilks' lambda = 0.790, $P \leq 0.001$) was a function of increasing nest tree height and density of woody plants. Classification of nest and paired sites into their correct group was 69% for Red-

TABLE 3. White-tailed Hawk (WTHA), Red-tailed Hawk (RTHA), Crested Caracara (CRCA), and paired random nest-site variables[a] that differed for each species in Brooks County, Texas, 2003–2004.

	WTHA	RTHA	CRCA	Random	
Variable[b]	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	$\bar{x}$ ± SD	*t*
CANOPYDIA	5.5 ± 2.1			6.9 ± 2.6	−2.70
TREEALV	88 ± 18			95 ± 10	−2.06
WOODY2	9 ± 5			11 ± 5	−1.88
15VERTHT	0.5 ± 0.3			0.6 ± 0.4	−2.21
NATGR1		5 ± 9		9 ± 12	−1.68
WOODDEN		15.7 ± 9.6		9.6 ± 6.9	3.20
WOODHT		5.8 ± 1.7		4.9 ± 2.6	1.82
TREEHT		10.1 ± 2.0		8.4 ± 2.4	3.39
NATGR!			16 ± 16	31 ± 24	−2.59
WOODDEN			9.9 ± 6.7	4.2 ± 6.3	3.04
WOODHT			3.5 ± 1.8	2.3 ± 1.8	2.35
TREEHT			5.6 ± 1.7	4.6 ± 1.7	2.38

[a] Differences between raptor and random nest-site variables are significant ($P \leq 0.10$).

tailed Hawk nest sites and 74% for random sites, giving an overall correct classification of 71%, which was 21% greater than the 50% prior probability of correct classification indicating a 30% overlap between used and available habitat.

Four nest-site variables differed ($P \leq 0.10$) between Crested Caracara nest sites and paired, random sites. Crested Caracara nest sites had less native grass, more woody plants that were taller, and taller nest trees. The DF (eigenvalue = 0.352, Wilks' lambda = 0.740, $P = 0.004$) was a function of decreasing nest tree height and number of woody plants, and increasing native grass cover. Classification of nest and paired sites into their correct group was 79% for Crested Caracara nest sites and 75% for random sites, with an overall correct classification of 77%, a value that was 27% greater than the 50% prior probability of classification, which indicates a 23% overlap between used and available habitat.

DISCUSSION

White-tailed Hawks have been described as nesting in short trees in areas with little woody cover in native grass–forb prairie interspersed with patches of bare ground (Stevenson and Meitzen 1946, Farquhar 1986, Kopeny 1988). We found White-tailed Hawk nests in savannas dominated by native grasses and forbs with scattered shrubs and trees. Nest tree heights in our study (3.9 m) were similar to the 2.5–3 m heights reported by Stevenson and Meitzen (1946). White-tailed Hawks have been reported to use isolated, thorny shrubs as nest substrates (Farquhar 1986, Kopeny 1988), but we found they use a diversity of species. These studies and our own results suggest White-tailed Hawks are intolerant of moderate to heavy (≥40%) woody cover. Increased thornscrub encroachment may reduce suitable nesting and, possibly, foraging habitat for White-tailed Hawks. The potential loss of habitat for this state-threatened species is a conservation concern.

Red-tailed Hawks nested in live oak mottes or mesquite-dominated tree lines, which provided the tallest trees available in the generally open landscape of mesquite savanna and Tamaulipan thornscrub of our study area. Nesting in generally open areas may release Red-tailed Hawks from their tendency to nest in the tallest trees in an area (Speiser 1990). Our findings are similar to those of others who indicated Red-tailed Hawk nest sites were characterized by more tree and woody cover with use of hardwood/deciduous trees as nest substrates (Titus and Mosher 1981, Toland 1990, Stout et al. 1998, Smith et al. 2003).

Crested Caracaras used isolated, thorny shrubs and mesquite trees for nest substrates, but the substrates were taller, wider, and more densely-branched than those used by White-tailed Hawks. Crested Caracara constructed nests near the middle of trees, and those trees had more live branches and leaves than those at White-tailed Hawk nests. We suspect nest placement and vegetation cover may have offered better concealment of Crested Caracara nests. Other researchers have also reported Crested Caracara nests as well-concealed and below the canopy of isolated thorny shrubs and mesquites (Dickinson and Arnold 1996, Rivera-Rodriguez and Rodriguez-Estrella 1998, Goldstein 2000).

The nesting habitat of these three species in our study area can be characterized as: (1) Red-tailed Hawks nested in the tallest trees in the area, near open savannahs, and had more tree cover than surrounding areas; (2) White-tailed Hawk nests were in thorny shrubs and mesquite trees at sites containing little (<20%) woody cover; and (3) Crested Caracara nested in bushy, thorny shrubs and surrounding habitats in mostly open grassland. Discrimination among the respective nest sites of the three raptor species was best made by four variables: nest tree height, native grass cover, percentage of the nest tree that was alive, and horizontal woody plant cover (Fig. 1). The high level of correct classification of each species' nest sites (89%) suggests these four variables are strong and reliable predictors. Complete separation of nest sites between White-tailed and Red-tailed hawks suggest nesting habitat is effectively partitioned by these two species. This partitioning may have evolved through preferences for nesting habitat. Crested Caracara nest sites shared characteristics of both of the other two species. Intra-specific tolerances or intolerances may also influence nest habitat partitioning between these species, but we have no data with which to assess this possibility. We do not know how the generally scavenging rather than active predatory behavior of Crested Caracaras may influence the intra-specific behaviors of this raptor community.

We did not present data on habitats used to forage for prey, but the patterns of nest site habitat use documented for these three species may be related to this important aspect of their life history. For example, Red-tailed Hawks typically live and hunt in woodland habitats with nearby open plains and prairie vegetation (Preston and Beane 1993). White-tailed Hawks hunt for prey in open coastal grasslands and semiarid brush (Farquahr 1992) while Crested Caracara are strongly linked to brushy habitats with widely scattered openings where they feed on carrion on the ground (Morrison 1996). It would be most informative for a future study to use our multivariate results from nesting habitat use for hypotheses to test for differences in foraging habitat among these three species.

All three species appear to use relatively open areas for nesting and, presumably, foraging. Habitat availability for all three species is likely to decrease as the Coastal Sand Plain region continues to undergo brush encroachment or conversion to agricultural production. These may be critical factors for conservation of White-tailed Hawks in particular because the population in the United States has not been adequately assessed. It is listed as a state threatened species throughout its geographic range in Texas. Crested Caracaras should benefit from conservation plans that maintain White-tailed Hawk habitat. The generally open landscape preferred by White-tailed Hawks should also benefit Red-tailed Hawks if oak mottes or other tall growing groves of trees are maintained.

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HYBRIDIZATION AMONG BUTEOS: SWAINSON'S HAWKS (*BUTEO SWAINSONI*) × RED-TAILED HAWKS (*BUTEO JAMAICENSIS*)

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ABSTRACT.—We report three cases of hybridization between wild Swainson's Hawks (*Buteo swainsoni*) and Red-tailed Hawks (*B. jamaicensis*) identified by using nuclear and mitochondrial DNA markers. The hybrid individuals were field-identified as Swainson's Hawks and sampled from Alberta, Canada (n = 2) and Utah, USA (n = 1). Nineteen nuclear microsatellite loci were used in a factorial correspondence analysis to create genotypic clusters of 468 Red-tailed and 357 Swainson's hawks. Three suspected hybrids were identified by an intermediate genetic position between the genotypic clusters of the two species, indicating a hybridogenetic composition. We examined mitochondrial control region sequence data to identify the maternal background of the putative hybrids; two of the hybrid specimens had Red-tailed Hawk mtDNA haplotypes and the third a Swainson's Hawk haplotype. These results suggest that hybridization between these two species may occur in their shared breeding range and can result in reciprocal hybrid offspring, barring any social, behavioral, or biological isolating mechanisms. *Received 30 October 2006. Accepted 23 February 2007.*

Hybridization is relatively common among birds with documented cases in ~9% of avian species (Grant and Grant 1992). The frequency of hybridization varies greatly among Orders. Hybrids are often artificially generated among Falconiformes for falconry (Bunnell 1986, Weaver and Cade 1991, Fox and Sherrod 1999), particularly within the genus *Falco* where Peregrine Falcon (*F. peregrinus*) × Gyrfalcon (*F. rusticolis*) hybrids are especially popular. Hybridization among wild raptors is less common, especially within the genus *Buteo* (Clark and Witt 2006).

Clark and Witt (2006) reported the first conclusive example of hybridization between native North American raptors of the genus *Buteo*: a Swainson's Hawk (*B. swainsoni*) × Rough-legged Hawk (*B. lagopus*) hybrid collected in Louisiana. We estimate sequence divergence between these two species based on the mitochondrial control region to range from 4.4 to 6.3% (mean 4.8%). Hybridization between these two species spans several well-supported species clades within the genus *Buteo* (Riesing et al. 2003). Hybridization between raptors has been infrequently reported and difficulty in identifying hybrid offspring in the field may result in underestimation of the extent of hybridization in the wild. We present molecular genetic evidence of three cases of hybridization between free-ranging Swainson's and Red-tailed hawks (*B. jamaicensis*) based on nuclear microsatellite genotypes and mitochondrial control region sequences.

METHODS

Sample Collection.—Samples of Swainson's (n = 357) and Red-tailed hawks (n = 468) were obtained from California to North Dakota, and Alberta to Texas between 2003 and 2005. White-tailed Hawks (*B. albicaudatus*, n = 47) were also sampled for outgroup comparison. Approximately 0.2 ml of blood was drawn via medial metatarsal venipuncture and two feathers were plucked from the breast of each bird. Blood samples were stored in 1.2 ml of Longmire's lysis buffer (100 mM Tris pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS) at ambient temperature until delivered to laboratory facilities where they were preserved at −80° C. Feather samples were

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stored in paper envelopes and kept cool and dry. Samples were collected from adults, juveniles, and pre-fledge young in nests by licensed raptor biologists, as well as from juveniles and adults treated at several wildlife rehabilitation facilities. All wild birds were leg-banded with U.S. Geological Survey bands and either released or returned to nests. Only one individual per presumed family group (nestlings and parents) was included in our sampling. Genomic DNA was isolated from 25 μl of the blood/buffer solution and from feathers using QIAGEN DNeasy kits (QIAGEN Inc., Valencia, CA, USA). DNA was stored at 4° C while in use and transferred to −20° C upon completion of genetic work.

Data Collection.—Each individual was genotyped at 19 microsatellite loci (BswA110w, BswD122w, BswA204w, BswA317w, BswD210w, BswD220w, BswA303w, BswB111aw, BswD234w, BswD310w, BswD313w, BswB220w, BswB221w, BswD327w, BswA302w, BswA312w, BswD107w, BswD127w, and BswD324w; Hull et al. 2007) in six multiplex PCRs following the conditions of Hull et al. (2007). PCR products were electrophoresed with a 3730 DNA Analyzer (Applied Biosystems Inc., Palo Alto, CA, USA). PCR products were visualized and scored with STRand (Version 2.3.69; Toonen and Hughes 2001).

Four-hundred sixteen base pairs of domain I of the mitochondrial control region were amplified via PCR in three putative hybrid samples (following amplification conditions in Kimball et al. 1999), a subset of Red-tailed (n = 5) and Swainson's hawks (n = 279), and one White-tailed Hawk using primer sets 16065F (Kimball et al. 1999) and H15414 (Bollmer et al. 2005). A recent phylogenetic study of the genus *Buteo* indicated strong nodal support for the monophyly of these three species based on two mitochondrial regions (ND6 and pseudo-control region) (Riesing et al. 2003). PCR products were cleaned of unincorporated primers and dNTPs using Ultraclean purification kits (MoBio, Carlsbad, CA, USA) and sequenced at the University of California Davis DNA Sequencing Facility using primers 14965F (J. M. Hull, unpubl. data) and H15414. Sequences were examined and aligned using SEQUENCHER (Version 4.5; Gene Codes Corporation, Ann Arbor, MI, USA).

Microsatellite Data Analysis.—Genotypic clusters were created using a factorial correspondence analysis (FCA) in the program GENETIX 4.05.2 (Belkhir et al. 2000). We used FCA to describe genotypic groups based on microsatellite allele frequencies, using the ordination of samples along varying factorial axes to visualize genetic similarity of the species clusters in two-dimensional space. Familial relationships among hybrid individuals from similar locations were assessed using a maximum likelihood approach as implemented in ML-RELATE (Kalinowski et al. 2006).

Control Region Sequence Analysis.—We used PAUP* (Version 4.0b10; Swofford 2003) for phylogenetic analyses using maximum parsimony (MP), maximum likelihood (ML), and distance analyses with *B. albicaudatus* designated as the outgroup. We used MRMODELTEST (Version 2.1; Nylander 2004) to choose the model of DNA substitution and parameter estimation for heuristic ML and distance analyses that best fit our control region sequence data. The product for hierarchical likelihood ratio (HKY + G) and Akaike information criterion (HKY + I) tests differed slightly. Both models were used in parameter settings, but the results did not differ in tree topologies or support. Nodal support was estimated for MP and ML trees using bootstrap searches (500 pseudoreplicates) and Bayesian posterior probabilities (10 million generations, 1 million burn-in, MRBAYES Version 3.1.2; Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003).

RESULTS

We obtained multilocus genotypes for 468 Red-tailed, 357 Swainson's, and 47 White-tailed hawks. Factorial correspondence analysis displayed distinct genotypic clusters for Red-tailed Hawks, Swainson's Hawks, and White-tailed Hawks with three individuals occurring intermediate to Red-tailed and Swainson's hawks (Fig. 1) indicating hybridogenetic genotypes. Two of these hybrid individuals were from the same geographic region. Maximum likelihood estimation of familial relationship indicated these two individuals have a probability 11.7 times greater for being unrelated than for being siblings.

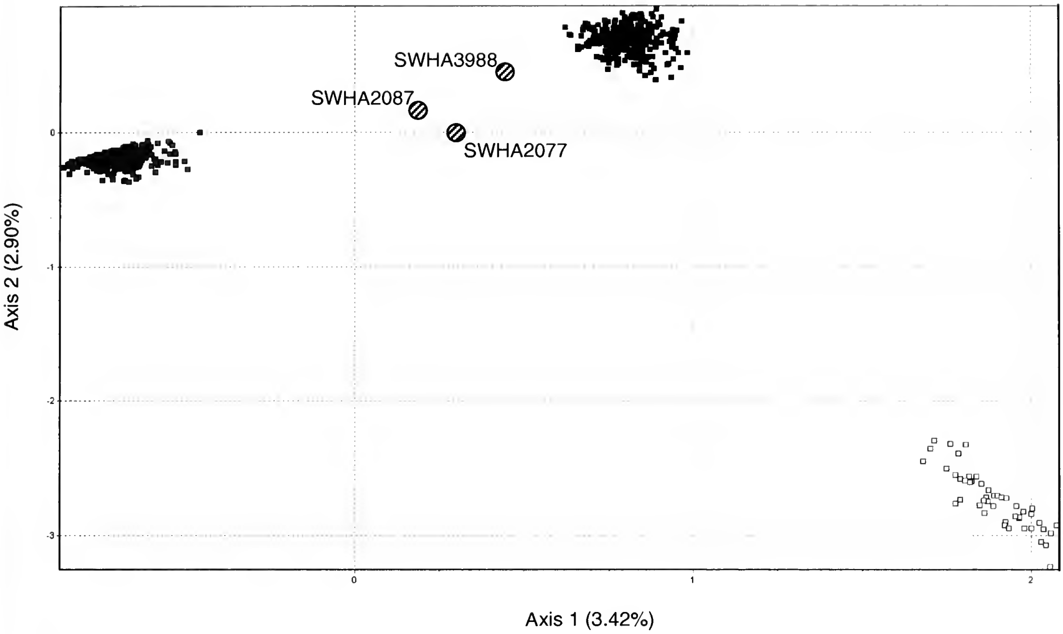

FIG. 1. Two-dimensional plot of the factorial correspondence analysis of multilocus genotypes for 357 Swainson's Hawks (black squares), 468 Red-tailed Hawks (gray squares), 47 White-tailed Hawks (white squares), and three Red-tailed Hawk × Swainson's Hawk hybrids (shaded circles).

Five Red-tailed, 279 Swainson's (where sufficient sample allowed microsatellite and mitochondrial sequence analysis), and one White-tailed hawk were sequenced at a portion of the control region. All sequences were archived in GenBank (accession numbers pending). We found no evidence of nuclear copies of the control region as replicate DNA sequences extracted from feathers and blood yielded identical sequences. There were no indels, double peaks or heteroplasmy observed in the electropherograms, and sequences aligned with previously published raptor control region sequences. We identified 33 haplotypes for Swainson's Hawks, one single haplotype for the five Red-tailed Hawk sequences, and one haplotype for the White-tailed Hawk among the 285 sequences. Fifty-seven of the 416 bp used in the analyses were variable and 39 were phylogenetically informative. Uncorrected sequence divergences between White-tailed Hawks and in-group taxa ranged from 7.21 to 8.17% (mean = 7.8%), and between Swainson's and Red-tailed hawks from 5.53 to 7.21% (mean = 6.49%). Uncorrected sequence divergences among Swainson's Hawk haplotypes ranged from 0.24 to 2.64% (mean = 1.14%).

Maximum parsimony, maximum likelihood, and distance analyses produced concordant tree topologies with insignificant differences at tip relationships within Swainson's Hawks (Fig. 2). Bootstrap analyses of phylogenetic trees suggested strong support for reciprocal monophyly of the Swainson's, Red-tailed, and White-tailed hawk clades (Fig. 2). Within each clade, however, there was little or no support for intraspecific geographic/genetic structure. Two individuals with intermediate microsatellite FCA assignments nested with Red-tailed Hawk haplotypes in a well-supported clade, and a third hybridogenetic individual nested within a monophyletic Swainson's Hawk clade (Fig. 2).

DISCUSSION

Microsatellite and mitochondrial data indicate that hybridization occurs between wild populations of Red-tailed and Swainson's hawks, and spans well-supported phylogenetic distances in the genus *Buteo*. Two of these samples were from juveniles at the Calgary

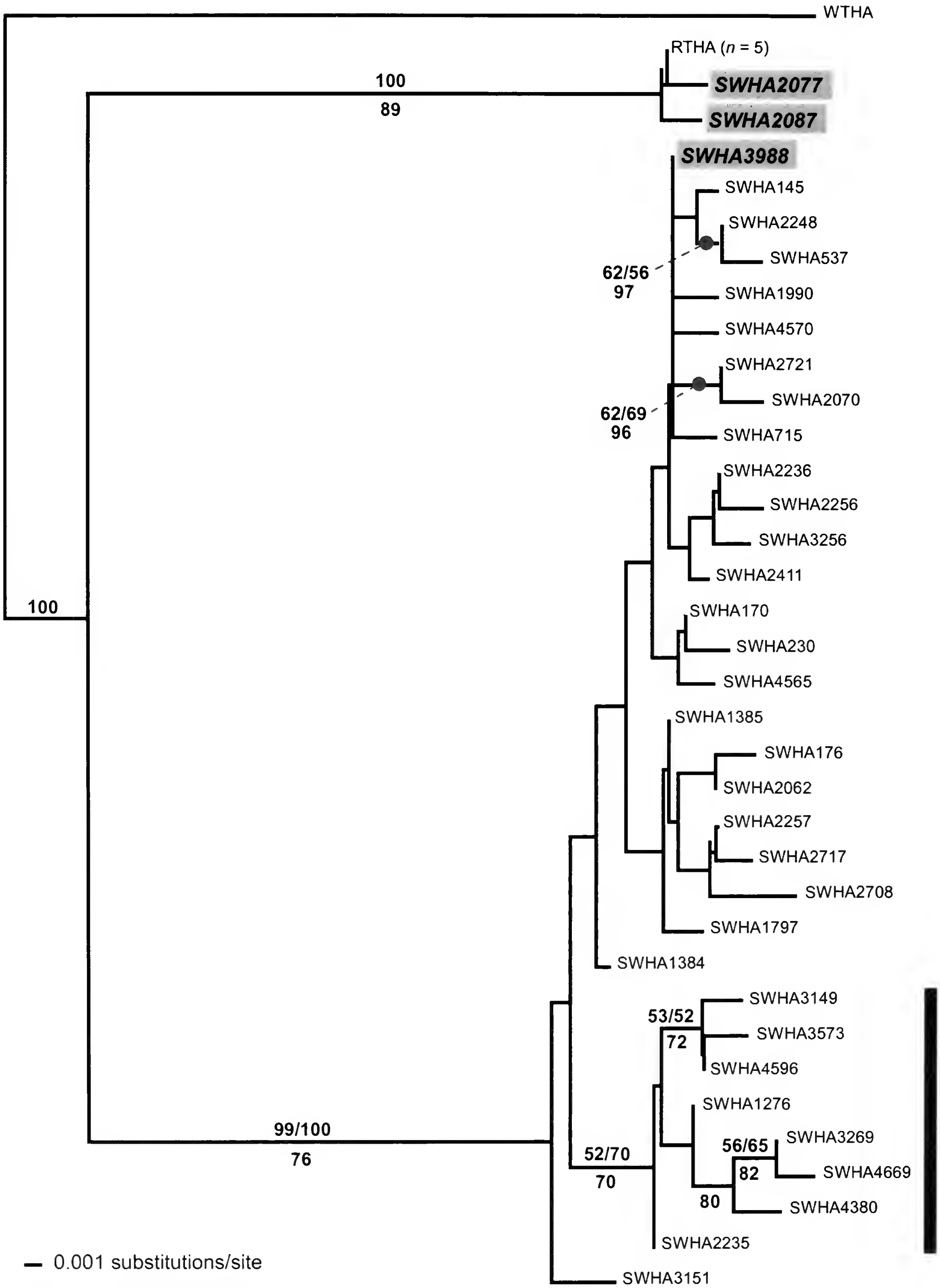

FIG. 2. Maximum-likelihood phylogram for 33 Swainson's Hawk (SWHA) mtDNA haplotypes, one Red-tailed Hawk (RTHA) haplotype, one White-tailed Hawk (WTHA) haplotype, and three haplotypes from hybrid individuals (bolded text and shaded). Two of the hybrids (SWHA2077 and SWHA2087) are nested in a well-supported clade with Red-tailed Hawks, and the third hybrid (SWHA3988) is deeply nested within Swainson's Hawks. Numbers above branches are parsimony/likelihood bootstrap values (500 pseudoreplicates); numbers below branches are Bayesian posterior probabilities. Marginal likelihood bootstrap values support some substructure within SWHA (shaded vertical bar).

Wildlife Rehabilitation Society in Alberta, while the third was from a nestling in northwestern Utah. The two samples from Alberta appear unrelated indicating this data set reflects three separate hybridization events. The mitochondrial control region sequences identify the mother in two of these cases as a Red-tailed Hawk (Alberta) and, in the third case, the mother was a Swainson's Hawk (Utah), demonstrating that hybridization is possible for both species-gender combinations. We report a small sample size of hybrid individuals, but the results suggest that intrinsic pre- and post-zygotic reproductive isolating barriers may not be uniformly present between Swainson's and Red-tailed hawks. These findings also imply courtship and mating behavior differences may not prevent interspecific breeding in all cases, nor does morphology. The average sizes of males and females of both species are comparable (Preston and Beane 1993, England et al. 1997), and resulting pairings would retain the natural intraspecific reverse sexual size dimorphism.

Nest-site observations in Utah confirm our genetic evidence of hybridization. Early in the nesting season, HawkWatch International crews observed a Swainson's Hawk and a Red-tailed Hawk switching incubation duties at the nest. The chick was banded several weeks later, during which time the Swainson's Hawk was flushed from the nest and defended the territory along with a Red-tailed Hawk, presumably its mate. Upon fledging, the hybrid offspring appeared phenotypically similar to a Swainson's Hawk with no obvious Red-tailed Hawk characteristics. In contrast, both hybrids from Alberta were phenotypically similar to Red-tailed Hawks.

Clark and Witt (2006), following Short (1969), speculated that limited overlap in the distribution of breeding Rough-legged and Swainson's hawks may facilitate hybridization through the absence of behavioral barriers to reproduction that exist among species with broad range overlap. The breeding range of Swainson's Hawks is overlapped entirely by that of Red-tailed Hawks (Preston and Beane 1993, England et al. 1997). Two of the hybrid samples were collected from the northern periphery of Swainson's Hawk range and the third was in the geographic center of the ranges for both species. Ecological or behavioral circumstances that promoted Swainson's Hawk × Red-tailed Hawk pairings remain unknown.

It is not known if hybrid offspring of Red-tailed and Swainson's Hawks are fertile or if other barriers exist to introgression. We do not know the lineage/genetic composition of the hybrids nor their parents, which may be of pure or mixed ancestry. It is unlikely that widespread hybridization is ongoing given the low frequency found in this study; among the sample of 825 individuals (468 Red-tailed Hawks, 357 Swainson's Hawks) only 0.004% were hybrids. The low number of hybrids may indicate mating preferences for conspecifics, or it may be that hybrids are less fit than the parental species. Given the markedly different migratory behaviors of Red-tailed Hawks (partial, moderate-distance migrant) and Swainson's Hawks (complete, long-distance migrant), hybrids with intermediate migratory behaviors may not reach optimal wintering and breeding areas and may be at a selective disadvantage. This would be particularly true from a Swainson's Hawk perspective as the vast majority of the species winters in central Argentina.

The extent of hybridization between Swainson's and Red-tailed hawks at the population level, and its causes, is unknown. The particular natural or anthropogenic conditions that promote hybridization also remain unidentified. If hybridization and introgression continue to occur at the low levels observed in this study, genetic diversity and distinctiveness may not be severely impacted. However, if environmental conditions promoting extensive Swainson's Hawk × Red-tailed Hawk hybridization become common, genetic introgression may become an important conservation concern. Currently, the presence of distinct genotypic clusters in the FCA suggests that hybridization and introgression are not resulting in a deterioration of genetic distinctiveness between Swainson's Hawks and Red-tailed Hawks.

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SURVIVAL OF RADIO-MARKED MALLARD DUCKLINGS IN SOUTH DAKOTA

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ABSTRACT.—Numerous researchers have investigated survival of Mallard (*Anas platyrhynchos*) ducklings, but few have modeled survival of ducklings radio-marked at hatch relative to time-dependent factors. We estimated survival of 48 radio-marked ducklings for two study sites (Oakwood and Mickelson) in eastern South Dakota during summers 1998–1999. Our best-approximating model of survival indicated duckling age, study site, precipitation, and the interaction of study site and precipitation influenced survival. Survival of ducklings to 30 days was 0.42 at Oakwood (95% CI, 0.13–0.67) and 0.77 at Mickelson (95% CI, 0.42–0.92). Duckling mortality was 31.9 and 1.6 times more likely for each 1 cm of precipitation at Oakwood and Mickelson, respectively. We suggest this difference was partially attributable to greater cover of emergent vegetation at Mickelson, which potentially reduced body heat loss via evaporative cooling. Our best model also indicated daily survival increased with duckling age. Models containing daily minimum temperature received little support ($w_i \leq 0.01$) indicating the covariate had negligible influence on daily survival of ducklings. *Received 7 September 2006. Accepted 12 February 2007.*

Duckling survival may critically influence Mallard (*Anas platyrhynchos*) recruitment in the Prairie Pothole Region (PPR) of North America (Cowardin and Johnson 1979, Johnson et al. 1987, Sayler and Willms 1997), potentially accounting for 14% of variation in the finite population growth rate (Hoekman et al. 2002). Cowardin et al. (1985), in an intensive study of Mallard breeding ecology in the late 1970s, identified duckling survival as one of the least understood components of recruitment. Several researchers have estimated Mallard duckling survival in the PPR since this pioneering work (e.g., Talent et al. 1983, Rotella and Ratti 1992, Sayler and Willms 1997, Gendron and Clark 2002).

Duckling survival is commonly estimated by radio-marking females prior to hatch and periodically relocating the female and brood to count number of ducklings surviving. However, assumptions must be made to use this method. Duckling counts may be inaccurate (Orthmeyer and Ball 1990, Mauser et al. 1994, Davis et al. 1999) due to secretive behavior of females and ducklings during brood rearing (Sedinger 1992:121). Ducklings are known to leave their natal brood and join other broods (i.e., brood mixing; Mauser et al. 1994), and ducklings absent from a count must be assumed dead. Similarly, if the brood female dies, the entire brood is assumed dead, but ducklings can survive independently or mix with another brood even at a relatively young age (Davis et al. 1999, Stafford et al. 2002); however, when considered, such instances do not bias survival estimates (Flint et al. 1995). Advances in telemetry equipment have allowed radio-marking of individual neonate ducklings (Mauser and Jarvis 1991). Despite these advantages, few published studies have reported survival of radio-marked day-old Mallard ducklings (Krementz and Pendleton 1991; Mauser et al. 1994; Howerter et al. 1996; Stafford et al. 2002; Krapu et al. 2004, 2006). Only Krapu et al. (2004, 2006) examined survival relative to time-dependent covariates (e.g., daily temperature).

Modeling survival based on factors thought to influence duckling mortality has been a natural extension of earlier estimation efforts. Researchers have examined many covariates, but factors influencing duckling survival and associated effect sizes have varied among studies. Stafford et al. (2002) modeled the proportion of ducklings within broods surviving to ≥20 days post-hatch using brood counts in relation to coarse-scale covariates where the best model explained only 26% of the variation in survival. Predation was identified or

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suspected in only 42% of radio-marked duckling mortalities (Stafford et al. 2002:331) and several mortalities appeared to coincide with exposure to weather events (i.e., cold nights or heavy rains; Stafford 2000). Stafford et al. (2002) did not model survival of radio-marked ducklings using fine-scale weather variables with the potential to explain unidentified mortality agents. The objectives of our study were to: (1) use recently developed survival estimation techniques (i.e., Rotella et al. 2004) to model variation in survival of Mallard ducklings radio-marked at two study sites in eastern South Dakota during 1998–1999, and (2) relate our results to previous findings for other areas of North America.

METHODS

Study Areas.—We studied duckling survival within the Coteau des Prairie physiographic region of eastern South Dakota (Johnson et al. 1995, Johnson and Higgins 1997). The Prairie Coteau is a highland region between the Minnesota–Red River Lowland and James River Lowland. It is characterized by large numbers of wetlands and is used extensively by breeding and staging waterfowl.

Our study areas consisted of the Mickelson Memorial Wetland (hereafter Mickelson), a 400-ha marsh in southern Hamlin County (44° 36′ 00″, 96° 58′ 00″), and the Oakwood lakes complex (hereafter Oakwood) comprised of 2,330 ha of wetlands and adjacent uplands in northern Brookings County (44° 26′ 30″, 96° 59′ 00″).

Mickelson was a class IV (semipermanent) hemi-marsh (Stewart and Kantrud 1971) with extensive interspersed emergent cover consisting mostly of cattail (*Typha* spp.). Water control structures at Mickelson allowed water level manipulation, although stable levels were maintained during the study period. Few other wetlands were present near Mickelson. Oakwood was a mixture of class III (seasonal) and IV wetlands surrounding two large class V (permanent) lakes (Stewart and Kantrud 1971). Class IV wetlands were predominant due to abundant precipitation prior to and during the study period. Some bays of the two permanent lakes exhibited class IV characteristics. Most wetlands at Oakwood contained peripheral emergent vegetation of cattail, bulrush (*Schoenoplectus* spp.), and common reed (*Phragmites australis*).

Data Collection.—All broods in our study were hatched from overwater nesting structures (Stafford et al. 2002). We checked structures starting 10 May 1998–1999 for active Mallard nests and ascertained incubation stage by egg candling (Weller 1956). We returned to nests on the predicted hatch date to radio-mark ducklings. We selected two ducklings per brood at random and fitted them with modified Mauser subcutaneous prong and suture transmitters (Mauser and Jarvis 1991). Transmitters weighed 1.5 g with a range of 0.8 km and a battery life of ≥30 days (Advanced Telemetry Systems, Isanti, MN, USA). We fitted ducklings without transmitters with plasticine-filled aluminum leg bands (Blums et al. 1994, 1999), and captured and fit all attending hens (i.e., with or without radio-marked ducklings) with a 4.5-g radio transmitter attached via a subcutaneous prong and sutures (Pietz et al. 1995, Stafford et al. 2002).

We followed radio-marked ducklings to their brood-rearing wetland after they departed the nesting structure and sought locations daily using handheld Yagi and truck mounted null-peak antennas. We confirmed survival of ducklings (i.e., they were moving) via multiple triangulations or walking in with handheld equipment when visual observations could not be obtained. Survival of Mallard ducklings generally stabilizes by 30 days (Rotella and Ratti 1992, Mauser et al. 1994); thus, we monitored ducklings until 30 days post-hatch, loss of contact, or mortality.

We monitored ducklings most intensively from sunrise to 1000 hrs CDT and from 1800 hrs until dark, because waterfowl broods are most active during those times (Beard 1964, Ringelman and Flake 1980). We investigated status of radio-marked ducklings immediately if they were not close to the female to maximize the possibility of identifying timing and cause of mortalities. We examined duckling carcasses and the immediate vicinity of carcasses for signs of depredation. If we were uncertain of the specific day of mortality we used the last date the duckling was known to be alive to compute the survival interval in subsequent analyses.

Survival Estimation and Modeling.—Stafford et al. (2002) placed radio transmitters on

58 ducklings at 1-day post hatch during their study period. We censored 10 of those ducklings for our analysis; eight of these were marked at a third study site, of which all died, providing no variation in survival for modeling. We excluded the two other ducklings because of unverifiable inconsistencies in data recording. We estimated duckling survival to 30 days post-hatch using the nest survival model in program MARK (White and Burnham 1999, Dinsmore et al. 2002). This approach allowed us to model duckling survival as a function of group- (e.g., study site) and time-specific (e.g., daily precipitation) covariates. We used the nest survival model in MARK because the exact date of mortality was not known for all ducklings. This procedure only required an interval within which a duckling died instead of an exact date of mortality (White and Burnham 1999). The nest survival model estimated relationships of daily survival rates to covariates using a logit link function (Dinsmore et al. 2002). Daily survival rate (DSR) of a duckling on day *i* was modeled as:

$$\mathrm{DSR} = \frac{\exp\left(\beta_0 + \sum_j \beta_j x_{ij}\right)}{1 + \exp\left(\beta_0 + \sum_j \beta_j x_{ij}\right)},$$

where x_{ij} were values for *j* covariates on day *i*, and β_j are coefficients estimated from the data (Rotella et al. 2004).

We identified best approximating and competing models using Akaike's Information Criterion corrected for small sample size and overdispersion ($Q\mathrm{AIC}_c$) (Burnham and Anderson 1998; Anderson et al. 2000, 2001). We attempted to correct for overdispersion to account for dependence in survival among brood mates (*sensu* Flint et al. 1995, Dinsmore et al. 2002). However, the nest survival model in program MARK did not have developed goodness-of-fit tests (Dinsmore et al. 2002). Thus, we computed the overdispersion coefficient ($\hat{c} = 1.38$) by dividing the deviance by degrees of freedom from the model with most parameters (S. J. Dinsmore, pers. comm.). We recognize that estimating $\hat{c}$ from deviances may not be valid if deviances were not Chi-square distributed (White and Burnham 1999). Program MARK ranked models from least to greatest $Q\mathrm{AIC}_c$, and calculated the simple difference between the best approximating model and competing models (Δ_i), and respective model weights (w_i) (Burnham and Anderson 1998, Anderson et al. 2001).

Covariates.—We developed a set of *a priori* candidate models intended to explain variation in Mallard duckling survival and included four covariates in our candidate set. We interpreted importance of covariates by calculating 95% confidence intervals about parameter estimates or odds ratios (i.e., back-transformed parameter estimates).

1. Study site (SITE). The Mickelson and Oakwood study areas differed with respect to wetland size, vegetative cover, water permanency, and wetland density (Stafford 2000). Stafford et al. (2002) estimated duckling survival, based on periodic brood counts, was greater at Mickelson than at Oakwood. We hypothesized survival would differ between study sites and included SITE as a group effect in 7 of 12 duckling survival models.

2. Precipitation (PRECIP). Precipitation has been associated with mortality of radio-marked Canvasback (*Aythya valisineria*), Gadwall (*Anas strepera*), and Mallard ducklings (Korschgen et al. 1996, Pietz et al. 2003, Krapu et al. 2006). Pietz et al. (2003) and Krapu et al. (2006) coded precipitation as a binary variable (0 = no rain, 1 = rain), but we hypothesized that amount of rainfall would negatively influence survival in a continuous fashion. We used precipitation data (cm/day) from the weather station nearest each study site (Castlewood, South Dakota for Mickelson [16.7 km from site]; Brookings, South Dakota for Oakwood [19.6 km from site]) as a time-dependent continuous covariate in analyses.

3. Temperature (TEMP). Minimum temperature was negatively associated with survival of radio-marked Gadwall, Canvasback, and Mallard ducklings (Korschgen et al. 1996, Pietz et al. 2003, Krapu et al. 2006). We hypothesized that cold temperatures could predispose ducklings to attrition from cold stress, reduced food availability and growth or increased vulnerability to predation due to restricted mobility (Korschgen et al. 1996). We included daily low temperature (°C) obtained from the weather station nearest the study area

TABLE 1. Model selection results for survival of radio-marked Mallard ducklings in eastern South Dakota including the number of estimable parameters (K), -2 log likelihood score ($-2\log(L(\hat{\theta}))$), quasi-likelihood second order Akaike's information criterion ($Q\text{AIC}_c$), model weight (w_i), and quasi-likelihood deviance score (QDeviance).

Model	K	$-2\log(L(\hat{\theta}))$,	$Q\text{AIC}_c$	$\Delta Q\text{AIC}_c$	w_i	QDeviance
$S_{SITE+AGE+PRECIP+SITE*PRECIP}$	5	143.81	114.07	0.00	0.70	104.00
$S_{SITE+AGE+PRECIP}$	4	150.75	117.06	2.99	0.16	109.02
$S_{SITE+AGE}$	3	155.12	118.20	4.13	0.09	112.18
S_{AGE}	2	162.22	121.33	7.26	0.02	117.31
$S_{AGE+PRECIP}$	3	159.63	121.47	7.40	0.02	115.44
$S_{AGE+TEMP}$	3	161.88	123.10	9.03	0.01	117.07
$S_{SITE+PRECIP+SITE*PRECIP}$	4	159.97	123.73	9.66	0.00	115.68
$S_{SITE+PRECIP}$	3	166.24	126.25	12.18	0.00	120.22
S_{SITE}	2	169.32	126.46	12.39	0.00	122.45
$S_{SITE+PRECIP+TEMP}$	4	165.87	128.00	13.93	0.00	119.95
$S_{(.)}$	1	178.75	131.27	17.21	0.00	129.27
S_{PRECIP}	2	177.58	132.43	18.36	0.00	128.42
S_{TEMP}	2	178.48	133.09	19.02	0.00	129.07

as a continuous time-dependent covariate in some duckling-survival models.

4. Duckling age (AGE). An assumption of the nest survival model is that daily survival rates are constant over time, but this may not be realistic. For example, duckling survival may be least during the first week post-hatch (Talent et al. 1983, Cox et al. 1998, Gendron and Clark 2002, Hoekman et al. 2004). Therefore, we hypothesized that survival likely increased as age of ducklings increased and included daily duckling age as a covariate in some models of duckling survival to control for the effect of this possible relationship.

RESULTS

We included 48 radio-marked ducklings from 24 broods in survival analyses (n = 22 [Mickelson] and 26 [Oakwood]). The best approximating model was 3.0 $Q\text{AIC}_c$ units from the second-best model, accounted for 70% of the w_i, and included the main effects of AGE, SITE, and PRECIP, as well as an interaction between SITE and PRECIP (Table 1). This model indicated that ducklings were 31.9 (95% CI, 4.0–251.6) times more likely at Oakwood and 1.6 (95% CI: 0.3–9.6) times more likely at Mickelson to die for each 1 cm increase in daily precipitation ($\bar{x}$ = 0.1, range: 0.0–6.8 cm/day), although the latter confidence interval about the odds ratio included 1. Additionally, this model indicated that duckling survival increased with AGE ($\hat{\beta}_{AGE}$ = 0.13, SE = 0.05; 95% CI = 0.04–0.22). Based on the best approximating model, survival to 30 days was 0.77 (95% CI, 0.42–0.92) and 0.42 (95% CI, 0.13–0.67) at Mickelson and Oakwood, respectively (0.62 overall). Daily low temperature occurred in the sixth best model (TEMP; $\Delta Q\text{AIC}_c$ = 9.03 [Table 1]; range: 1–21° C), and the 95% confidence interval about the parameter estimate included zero ($\hat{\beta}_{TEMP}$ = −0.03, SE = 0.07; 95% CI = −0.17–0.10).

DISCUSSION

Precipitation negatively influenced duckling survival based on our best approximating model, but the effect was weaker at Mickelson than Oakwood (Table 1). Precipitation may influence duckling survival by increasing the energy demand of thermoregulation via evaporative cooling (Bakken et al. 1999). This increased energy expenditure may have sublethal effects leaving ducklings more susceptible to predation (Korschgen et al. 1996, Pietz et al. 2003). Thus, the possible effect of precipitation on survival in our study may be conservative. Pietz et al. (2003) documented a relationship between survival of Gadwall ducklings and an interaction between rain events occurring within 2 days of mortality and temperature, where the greatest survival was observed when conditions were warm (>10° C) and without rain. We cannot directly compare the effect of precipitation on duckling mortality with these findings because our covariates were scaled differently, and our best approximating model did not include an interaction with temperature.

The negative effect of precipitation was markedly stronger at Oakwood. Broods at Mickelson used a large (400 ha) semipermanent marsh with interspersed emergent vegetation (~60% cover; Stafford et al. 2002), whereas ducklings at Oakwood spent most days on wetlands with <25% emergent cover (Stafford et al. 2004). It is possible precipitation had little influence on survival at Mickelson due to extensive emergent cover, which provided better thermoregulatory conditions during rain events. Wetland vegetation may reduce heat loss in Mallard ducklings due to wind (Bakken et al. 1999). We speculate increased cover might reduce heat loss from evaporative cooling by lessening exposure to precipitation. Alternatively, previous research indicated that rain events may inhibit emergence of chironomid larvae, an important food source for Mallard ducklings (Nelson 1989). This situation may be especially important if ducklings require increased energy to maintain homeothermy during cool, wet periods.

As hypothesized, results of our best model indicated duckling survival was positively associated with AGE. Indeed, the relationship between duckling survival and increasing age is well documented (Talent et al. 1983, Orthmeyer and Ball 1990, Mauser et al. 1994, Cox et al. 1998). Our inclusion of AGE in models addressed an assumption of the survival model (i.e., constant daily survival) and effectively controlled a source of variation in duckling survival, similar to the use of a covariate in analysis of covariance.

Korschgen et al. (1996), Davis (2001), Pietz et al. (2003), and Krapu et al. (2006) reported negative influences of precipitation, colder temperatures, or both on survival of radio-marked ducklings. Previous modeling efforts either categorized temperature above and below some threshold (e.g., 10° C; Pietz et al. 2003) or averaged minimum temperatures for the exposure day and two previous days (Davis 2001, Krapu et al. 2006). Our models including temperature may not be directly comparable with previous findings. However, we found that temperature within the range observed in this study did not considerably influence daily survival.

Stafford et al. (2002) attributed 58% of deaths of radio-marked ducklings to unknown causes and speculated these deaths were caused by exposure. We found precipitation events negatively influenced daily survival of ducklings; therefore, exposure due to precipitation events may have accounted for a large proportion of unknown and total mortalities. If tenable, this result is in contrast to findings from other duckling survival studies, where predation was the leading cause of death for Mallard ducklings in northeastern California (90%; Mauser et al. 1994) and North Dakota (89%; Krapu et al. 2004), Wood Duck (*Aix sponsa*) ducklings in Mississippi (81%; Davis 2001), and Gadwall ducklings in North Dakota (86%; Pietz et al. 2003). Furthermore, Pearse and Ratti (2004) found that 30-day Mallard duckling survival was 1.6 times greater on sites where mammalian predator density was experimentally reduced. Our situation was not entirely unique; Krementz and Pendleton (1991) also attributed few (16%) mortalities of radio-marked Mallard ducklings to predation on Chesapeake Bay.

Our results are not subject to the assumptions necessary for studies where only brood females were marked, but certain assumptions and caveats must be made. All ducklings in our study hatched in overwater nesting structures. Our estimates may be biased high in comparison to ducklings hatched from upland nests if the length of the initial overland movement adversely affects survival of Mallard ducklings (Ball et al. 1975, Rotella and Ratti 1992; but see Talent et al. 1983, Dzus and Clark 1997, Gendron and Clark 2002). Duckling survival also may be influenced by radio-marking (Pietz et al. 2003, Krapu et al. 2004). Krapu et al. (2004) increased 30-day duckling survival rates by 0.16 to account for transmitter effects. Stafford et al. (2002) detected no difference in survival between radio-marked and unmarked ducklings within years and sites, and we detected no difference in survival between radio-marked and unmarked ducklings when years and sites were pooled ($\chi^2_1 = 0.86$, $P = 0.353$). Thus, we did not account for transmitter effects in the current analysis and our survival rates may be considered conservative if transmitters negatively influenced survival.

Duckling survival was greater at a site with extensive interspersed emergent vegetation, possibly the result of reduced thermoregulatory stress. Management for interspersed emergents was possible at Mickelson because water control structures allowed for periodic drawdown. Placement of water control structures in larger restored wetlands could allow for improved management of emergent cover, but these efforts are costly and perhaps not efficient or predictable in promoting quality brood habitat over a large spatial extent. Thus, we suggest future research to investigate the potential effect of varying amounts and juxtaposition of emergent cover on duckling survival in managed wetlands.

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MALE BEHAVIORS OF SOCIALLY MONOGAMOUS TIBETAN EARED-PHEASANTS DURING THE BREEDING SEASON

XIN LU[1]

ABSTRACT.—The social behavior of free-living male Tibetan Eared-pheasants (*Crossoptilon harmani*) is described during their breeding season at a site near Lhasa, Tibet. Four types of male-male interactions were identified. (1) Mate guarding. A male maintained vigilance behavior near his partner. (2) Evading. A male urged the female to avoid other breeding males. (3) Lateral display. A male laterally presented his body to another male and the latter postured submissively. On a few occasions, displaying males escaped alone and dominant males attempted to copulate with mates of these males. (4) Driving. A male violently drove off any males that came too near his mate. These behavioral types emerged as pair members associated in groups in early spring, became extensive as pair bonds intensified, and disappeared with hatching. Paired males occasionally displayed to subadult males, but no display activity was observed between subadult males. These interactions were unidirectional for a group in which all male members were individually identified and revealed a linear dominance hierarchy among the males. I believe that mate-guarding was to detect and evading was to escape the high-ranking males, which potentially obtained (through displaying to lower-ranking males) extra-pair copulations. Advertising quality to impress/intimidate opponents and to attract additional females is likely the underlying reason for male-male display. My observations provide an interesting example of how males behaviorally respond to conflict between gregariousness and maintenance in a socially monogamous mating system. *Received 5 October 2006. Accepted 29 January 2007.*

Pheasants (Phasianidae) exhibit little spatial movement throughout the year and many species are social. Almost all existing descriptions of their social behaviors were established in captive conditions (Kruijt 1964, Wood-Gush 1971, Sullivan 1992). Numerous experimental studies have been conducted within a framework of sexual selection of socially polygynous species including Cabot's Tragopan (*Tragopan caboti*) (Islam and Crawford 1998), Ring-necked Pheasant (*Phasianus colchicus*) (Mateos 1998), Red Junglefowl (*Gallus gallus*) (Zuk et al. 1990, 1995; Collias and Collias 1996; Johnsen et al. 2001) as well as its domesticated form, the domestic fowl (Guhl et al. 1945, Wood-Gush 1971, Graves et al. 1985). Intensity and dynamics of social interactions are affected by the ecological and social environments in which animals have evolved. Thus, there is a clear need to describe the social behavior of pheasants in their natural habitats, especially for socially monogamous taxa.

Among the Phasianidae, *Crossoptilon* is one of the two genera that possess both sexual plumage monomorphism and monogamy, and its member species exhibit the strongest non-breeding gregariousness (Johnsgard 1999). The Tibetan Eared-pheasant (*Crossoptilon harmani*), which is endemic to the Tibetan plateau, belongs to this genus. It has been shown these birds live in social groups throughout the non-breeding season in the Lhasa Mountains, Tibet (Lu and Zheng 2002). Groups disperse during the breeding season, and adult males and females (sexually mature at 2 years of age) establish monogamous mating bonds. A pair produces one brood per year. Females lay one egg every 48 hrs from mid-April to early June and undertake incubation alone after the last egg is laid. Both parents provide care for their precocial chicks after the brood hatches (Lu and Zheng 2003).

Tibetan Eared-pheasants inhabit shrubby vegetation in the Lhasa Mountains and face a shortage of suitable habitats for night roosting and nesting (Lu and Zheng 2003). As a result, all members of a group use a roost (alpine willow [*Salix sclerophylla*] patches, <1,500 m^2 in size) year round even through monogamous mating pairs have been established and clutches have been initiated (nearest distance between two neighboring nest-sites = ~100 m); these pairs frequently meet both in roosts and in nesting habitats.

Extra-pair fertilizations occur commonly in birds (Birkhead and Møller 1992), especially those with monogamy (Petrie and Kempen-

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aers 1998). Questions arise regarding how males behaviorally resolve the conflict between gregariousness and minimization of paternity loss. Further, how do they seek to copulate with additional females and synchronously restrict attempts of extra-pair copulations from other males? I address these questions by: (1) describing social behaviors among breeding male Tibetan Eared-pheasants in a free-ranging population, (2) investigating the social circumstances in which male-male interactions occurred, and (3) explaining these functions in terms of sperm competition.

METHODS

Field work was conducted in Xiongse Valley (91° 40′ E, 29° 27′ N) in the Lhasa Mountains, Tibet, during the 1996 breeding season. The vegetation in the study area is characterized as scrub and meadow, and occurs across an altitudinal range from 3,980 to 5,200 m asl.

Tibetan Eared-pheasants are the only pheasant species in this region. Little was known of the species' social system before I conducted this study. Therefore, I investigated all aspects of their social behavior. Observations were made of three groups. Each of these used a year-round roost and regularly visited a Tibetan nunnery for additional food from late fall until incubation commenced. The nunnery and roosts provided several 'rendezvous' sites where group members interacted and most field observations were made. The birds were accustomed to the presence of people, were well protected by local Buddhists, and allowed themselves to be followed at distances of 5–10 m for extended periods.

Individual identification of all group members was possible for only one group (focal group) that roosted near the nunnery. I captured birds in this group by attracting them with food to walk into a 1.5-m-long string foot snare trap on the ground (the opposite end of the string was in my hand which I pulled to trap the bird's leg) and marked them with colored leg bands. Capture and marking took 2–5 min for each bird and had little adverse effect on the birds' behavior. Gender and age (adult and first-year subadult) could be reliably assigned from observation of leg-spur length and bill coloration (Lu and Wu 2003). Three individuals in the focal group were marked prior to, and six were marked during, the pairing period; a few unmarked individuals were recognizable from their plumage features. The group consisted of five breeding pairs plus two subadult males at commencement of the pairing period.

I began monitoring the birds in late February before groups dispersed. Field observations (~20–30 m from the birds to avoid any possible disturbance) were made for a few hours almost every day mainly in the morning or afternoon or throughout the day. During ~400 hrs of observations, I described and classified male social behaviors, recorded occurrence of each type of behavior, and identified the individuals involved when possible. The procedure was repeated when breeding males were in subgroups (one breeding male plus at least one other male) before final dispersal of the groups (31 Mar–17 Apr, pair information period), or of males that rejoined groups after females had started incubation (13 May–9 Jun, incubation period). I randomly located one male and followed him when males were in a separate male-female pair or alone (18 Apr–12 May, pair maintenance period). Each time the focal male met another male, I identified the rival and his mating status, and recorded the type of interaction between them. It was not possible to identify both males that interacted in all cases because of either my distance from the birds or dense cover. I recorded 347 male-male encounters during this study. The nests of four pairs of the focal group were located (two during incubation and the other two after hatching). The onset of incubation was assigned for all five pairs as the first day males were not accompanied by their mates.

RESULTS

Mate Guarding.—This occurred when two paired males were not in direct visual contact. A male stayed close to his partner (≤5 m) frequently scanning (with his head up and down) or remaining vigilant (with his head up to watch the surroundings) (Fig. 1A) while the female spent more time feeding. The female was more likely to lead the pair with the male following closely. In the evening, the male followed his mate to the roost and perched in trees behind her. He perched near her (<1 m) during the night and excluded others. At dawn

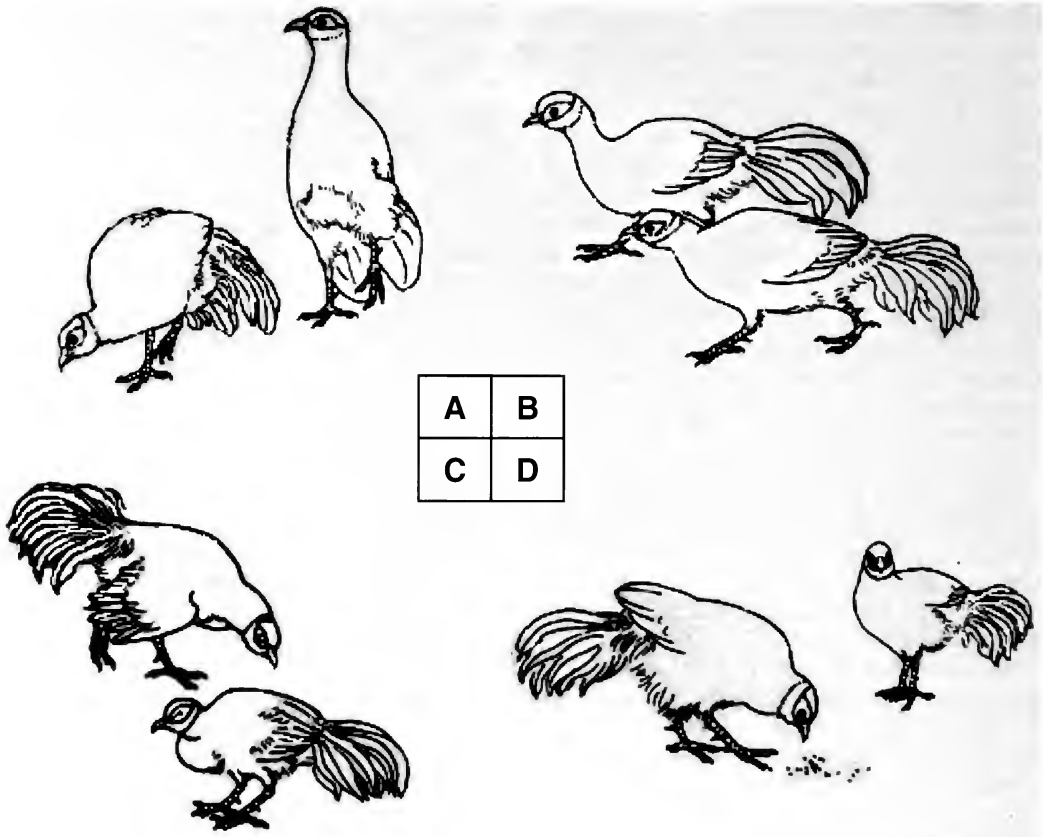

FIG. 1. Schematic representation of the behavior of male Tibetan Eared-pheasants based on photographed and video-taped sequences in the field. (A) Mate guarding, (B) Evading, (C) Lateral display, and (D) Feeding courtship.

the male usually became active earlier and flew to the ground calling his mate, which still slept or preened on the perch.

Evading.—Once a male caught sight of another male that displayed to him from a distance, he hurried his mate (often by pecking near or at her foot) and "urged" her to quickly depart. The male ran behind her closely, giving a low vocalization and sometimes scratching his bill against the ground. The female apparently cooperated with the male (Fig. 1B).

Male-male Lateral Display.—This occurred when two males happened to meet or a male actively approached another that did not leave the area. Ritually, a male stood or walked sideways towards the opponent male that had evaded him earlier with his head lowered, facial wattles enlarged, wing nearest the opponent spread almost to the ground and tail fanned, and giving low and continuous calls. The opponent responded to this display submissively, crouching to appear smaller than normal, often closing his eyes and preening as if in a resting posture, while on some occasions giving alarm calls or picking at something on the ground (Fig. 1C). Displayers did not beat the rival. Instead, in a few cases (3 of 162 displays), they pecked at a small food item or stone on the ground to attract the attention of the male to which the display was directed. This display also frequently occurred in roost trees where the normal pattern observed on the ground could not be followed.

The variation in duration of display varied from 5 to 1,500 sec. The longest record occurred near a nest site where the breeding male vigorously displayed to a solitary adult male, seemingly to prevent the latter from approaching his mate that was laying.

During male-male display, females of both males involved stood or foraged nearby (often within 5 m), showing no special responses to the behavior of the males.

Driving.—This occurred when a male violently drove and even chased any males that came too near his mate. This behavior was usually performed on the ground near roosts or at roost trees.

Interactions Between Breeding and Non-breeding Males.—Lateral display or driving from breeding male to subadult male was performed similar to interactions between breeding males. However, during the initial encounter, subadult males did not escape the breeding males. At times, breeding males accompanied by mates tolerated a subadult to be present during the day or night in the roost trees.

Interactions Between Non-breeding Males.—No social interactions characteristic of breeding males were observed between subadult males.

Male-female Lateral Display.—A male performed lateral displays towards a female in the same way as towards other males. This behavior was observed only during the earlier stage of the breeding season. The females always became panicky and tried to escape. Thus, these displays were short (<20 sec).

Courtship Display and Copulation.—Copulation often followed a feeding courtship typical of pheasant species. In this behavior, a male repeatedly pecked at (but did not attempt to eat) a food item or other objects, such as small stones, or at apparently nothing at all, on the ground while giving low calls to invite the nearby (≤5 m) female to feed (Fig. 1D). Once the female approached and ate the pecked object, the male attempted to mount her. If the male was not rejected, he would succeed in copulation. At times, a male performed copulation attempts without feeding courtship.

Male Social Rank.—All observed male-male interactions occurred among members from the same group. A paired male neither avoided nor displayed towards, but rather fought with in some cases, males of other groups. These inter-group interactions are not within the scope of this paper. I found by evaluating the outcome of dyadic aggressive encounters of any two males from the focal group (Table 1) that at every encounter, a displaying male invariably displayed to a recipient, drove him off or caused him to evade the initial encounter, and not vice versa. Behavioral records from two individually identifiable males of a neighboring group also showed the consistency in direction of the interactions. The typical linear dominance hierarchy among male members of the focal group was: Male I → Male II → Male III → Male IV → Male V → Subadult male. The top male initiated more aggressive behaviors (66 of 105 sightings, or 62.9%; pooled data of different types of behavior) than expected based on the probability (33.3%) of his encountering the five other lower-ranking males and winning all encounters ($\chi^2 = 8.26$, df = 1, $P = 0.004$).

Social Organization Dynamics.—Neither the male-male nor male-female interactions (Table 2, Fig. 2) described were noted during field observations totaling ~400 hrs from winter until early spring before emergence of pair associations. Monogamous pair bonds formed in late March when birds were still associated in groups, about 25–30 days before clutch initiation. Male-male evading and lateral display were observed as soon as pair associations appeared in the groups. Occasionally a male forced his partner to leave the current group as a consequence of an elaborate approach by higher-ranking males. However, the pair rejoined the group after 5–15 min (but more than 30 min in three cases) and either pair members or both males seemed to ignore each other. This behavior made the pair associations detectable.

Pairs tended to separate from each other more frequently as groups gradually dispersed and remained independent longer. Unstable subgroups consisting of 2–3 pairs became the major social units during this period. Finally, breeding pairs remained away from each other. Males did not occupy defined territories but traveled with their social mates over the home range of the group. The pair-bond was maintained until females began incubation. During incubation, breeding males made little effort to guard their nests, but instead joined subadult males from the group to form bachelor groups, moving over the group home range.

Temporal Pattern of Male-male Behav-

TABLE 1. Frequency and direction of aggressive interactions[a] between six male Tibetan Eared-pheasants from one group during the 1996 breeding season.

	Initiator														
	Male I			Male II			Male III			Male IV			Male V		
Recipient	D	E	LD	D	E	LD	D	E	LD	D	E	LD	D	E	LD
Subadult male	+1	0	+1	+1	0	+5	0	0	+1	0	0	+1	0	0	+2
Male V	+5	+1	+13	+7	+2	+4	0	+1	+2	0	+1	+1			
Male IV	+1	+4	+4	0	+1	+1	0	+2	+2						
Male III	+1	+4	+4	+1	+1	+3									
Male II	+1	+21	+5												
% of a behavior in all records of the behavior	50.0	78.9	55.1	50.0	10.5	26.5	0	7.9	10.2	0	2.6	4.1	0	0	4.1

[a] D = driving, E = evading, LD = lateral display, + = winning an encounter, 0 = no interaction.

iors.—Mate guarding was less obvious early in the breeding season when more than one pair associated together and was clearly observed when a pair temporarily or finally separated from other group members.

When males occurred in a group or subgroup during the early breeding season, their interactions at each encounter were relatively weak in terms of frequency of occurrence (10.1% of 159 evadings, 14.2% of 162 displays, and 19.2% of 26 drivings). Aggressiveness increased markedly (89.9, 64.1, and 80.8% of all observations for each behavior, respectively) when all pairs remained apart from others ($\chi^2 = 116.73$, df = 1, $P < 0.001$, for pooled data of the three types of behavior). If at least one of the two breeding males was accompanied by a mate, evading or lateral display would occur.

Once females were incubating, neither driving nor evading was observed. Lateral displays became rare and disappeared by the time chicks hatched (21.7% of all observations, $\chi^2 = 24.51$, df = 1, $P < 0.001$). Length (sec) of lateral displays, a measure of the intensity of aggressive interactions, significantly differed among the three stages of a reproductive cycle even excluding the exceptional example of 1,500 sec during the pair maintenance period (Kruskal-Wallis one-way ANOVA, $H = 18.41$, df = 2, $P < 0.001$, Fig. 3). It was longest during pair maintenance (138 ± 155 SD, 2–600 sec, $n = 39$), shortest during female incubation (34 ± 60, 2–240 sec, $n = 23$), and intermediate during the pair formation period (65 ± 76, 4–270 sec, $n = 14$).

Occurrence of Male-female Interactions.—Male-female lateral displays were infrequent with only six records obtained before groups dispersed. In each case the female displayed to panicked, and avoided the male.

I saw one successful and seven attempted within-pair copulations, five of which were induced by courtship feeding and three by direct mounting. These copulatory interactions were male-initiated, four occurring before and the remaining four (including the successful attempt) after pair bonds became independent.

The male on the receiving end of the display adopted a submissive posture during most male-male lateral display scenarios. Neither male showed special behavior towards their own female or those of their opponents.

TABLE 2. Occurrence of male behavior in Tibetan Eared-pheasants at different pairing stages.

	Pair formation	Pair maintenance	Female incubation
Between breeding males			
Mate guarding	Less obviously	Strongly	
Driving	Occasionally	Occasionally	No record
Evading	Occasionally	Almost in any case	No record
Lateral display	Less often	Almost in any case	Occasionally
Between breeding and subadult males			
Driving	No record	No record	No record
Evading	No record	No record	No record
Lateral display	Rarely	Rarely	Rarely
Between breeding male and female			
Lateral display	Occasionally	No record	
Within-pair copulation attempt	Rarely	Rarely	
Extra-pair copulation attempt	No record	Rarely	

In four (2.5%) of 162 displays, the male on the receiving end of a display fled in alarm without being followed by their mates. Immediately after this occurred, the displaying male attempted to copulate with the additional females by direct mounting. All of these attempts were rejected.

DISCUSSION

Male-female lateral display, also called waltzing, is well known among most species of pheasants to serve as the male's mate attraction and copulation solicitation (Johnsgard 1999). Several experimental studies have detailed the implication of this ritualized courtship behavior (Zuk et al. 1990, 1995; Islam and Crawford 1998; Zhang 1998; Mateos and Carranza 1999). Surprisingly, lateral display between males has not been reported. Evading behavior described here is also novel among pheasants.

My field study of Tibetan Eared-pheasants demonstrated that most adult males stayed in the same group for at least 2 years during

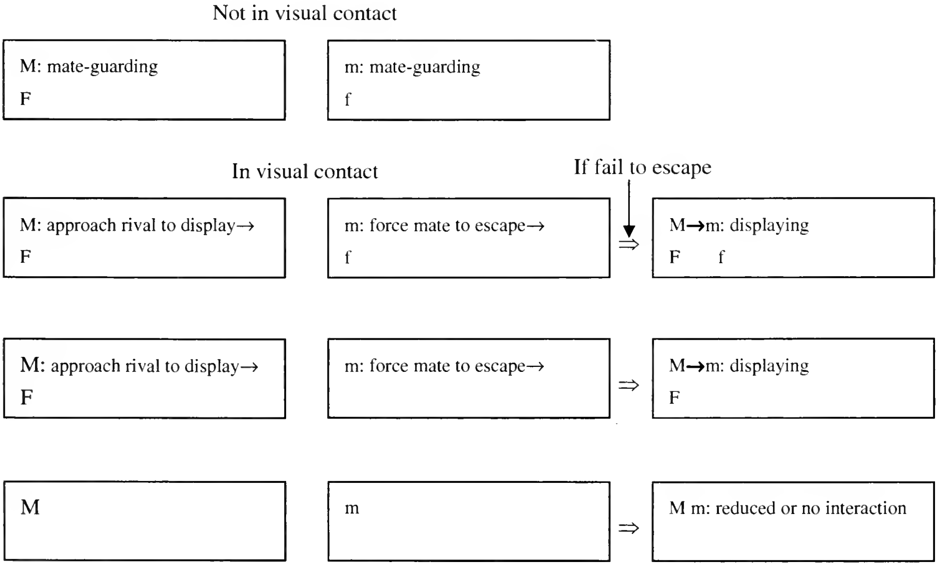

FIG. 2. Interactions between male Tibetan Eared-pheasants in relation to social rank and pair status. M = higher-ranking male, F = M's social mate, m = lower-ranking male, and f = m's social mate.

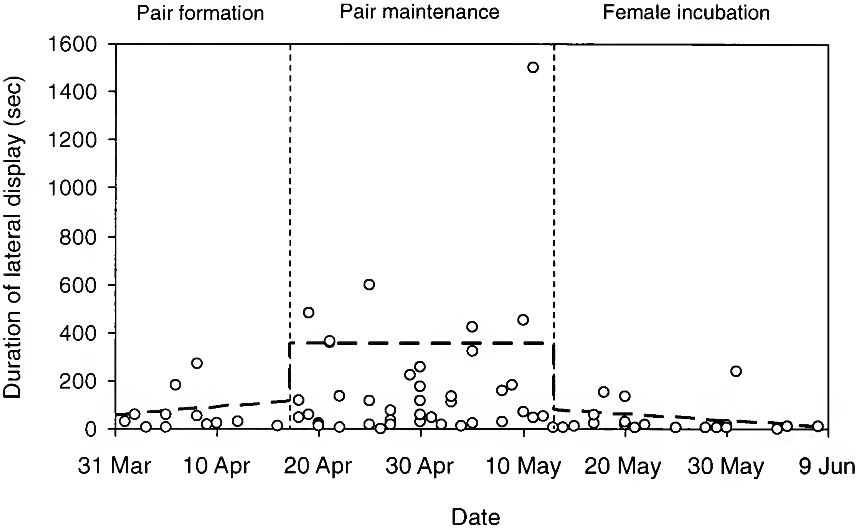

FIG. 3. Duration of lateral display (n = 77 observations, not including those at roost trees) between male Tibetan Eared-pheasants in relation to time of season (the dashed line was drawn by eye to show the temporal pattern). Duration of a display was from the onset of the first display bout to the end of the last bout, where a display bout was defined as uninterrupted display segments. At times a display was interrupted because the recipient moved away but the initiator often followed and resumed displaying. If two display bouts were separated by more than 5 min, they were considered to be different events.

which group males should already have established a dominance hierarchy. Therefore, the observed behavior is unlikely to have served to establish social dominance. Moreover, some pair bonds persist for at least more than 1 year (X. Lu, unpubl. data), and it seems unlikely that males used lateral display behavior for mate acquisition. Lateral displays were invariably unidirectional and caused the opponent to respond submissively leading me to assume this elaborate behavior was a male strategy of announcing and emphasizing their existing social status. This is consistent with the suppression hypothesis, where dominant individuals repeatedly condition subordinates to maintain their status (Dugatkin 1997, Forkman and Haskell 2004). A high dominance status, as the outcome of winning competitive encounters, should be an indicator of individual quality (Quarnström and Forsgren 1998). It is interesting to ask why dominant males frequently signify their quality in front of those lower in rank.

My observations showed that none of the male behaviors appeared prior to reproduction, but were performed intensively when breeding males became completely exclusive. These types of behavior are likely to be associated with sperm competition, which is expected to be strong in Tibetan Eared-pheasants because of their monogamous mating system, high nesting synchrony (as a result of a narrow reproductive window), and potentially high population density resulting from frequent encounters; these factors all promote competition (reviewed by Petrie and Kempenaers 1998). Males use two major strategies to ensure paternity: repeated copulation and mate-guarding (Birkhead and Møller 1992). Tibetan Eared-pheasants, which demonstrated infrequent within-pair copulations, adopt the latter.

For a male, mate-guarding should coincide with the fertile period of his mate and extra-pair copulation pursuits with females paired with other males (Birkhead and Hunter 1990). In Tibetan Eared-pheasants, the time a pair separated from others of the group should be the onset of the female's receptivity. Subordinates actively avoided contact with any dominant males at that time, suggesting the cuckoldry risk came from dominant males, or from their display attempts (Table 2, Fig. 2). Logically, evading and lateral display were context-dependent and it was through displays that higher-ranking males expressed their extra-pair copulation attempts. Males potentially obtained such opportunities as a result of their behavior. In addition, dominant males with mates displayed strongly towards single subdominant breeding males indicating this postural behavior had a function of paternity protection. The other available evidence I obtained, which included a relatively high tolerance among breeding males outside the assumed fertile period of females, strong male mate-guarding when females were receptive, reduced intensity of display between males whose mates were incubating, low levels of display of paired males toward subadult males, and no display between non-breeding males, provided further support for this hypothesis.

Male-male lateral display may be understood on the basis of the evolutionary and functional relationship between intra- and inter-sexual displays. Male-male competition and female preference are two major components of sexual selection. Berglund et al. (1996) considered that male status badges, which include behavioral traits, could evolve through male-male competition where outcomes direct female's choice to high-quality males. Kruijt (1964) confirmed that sexual courtship of Red Junglefowl is derived from between-young lateral display in a context of fighting. This congruity between males' threat to rivals and their attraction for mates in terms of performance and function is common (Bradbury and Davies 1987, Andersson 1994, Pryke et al. 2001). In most species of pheasants, including the Tibetan Eared-pheasant, male-female lateral displays are a male's tactic for attracting a mate and for soliciting copulation (Islam and Crawford 1998, Zhang 1998, Mateos and Carranza 1999, this study). Based on these empirical and theoretical lines of evidence, the congruity I observed between male-male and male-female lateral displays in Tibetan Eared-pheasant is expected. When a higher-ranking male advertised his quality, its purpose was to depreciate the opponent and to attract either the opponent's mate for extra-pair copulation or his own mate for strengthening the pair bond. Both females were present during male-male displays and were able to gain information on strength and dominance of either male. Evidence from Ring-necked Pheasant (Mateos and Carranza 1999), Red Junglefowl (Parker and Ligon 2002), and domestic fowl (Salomon et al. 1966) has shown that lower ranking males become less attractive to females in the presence of a dominant male. Since male-female lateral displays are prevalent among the Phasianidae, I predict that male-male displays could be more widespread than presently known.

Both mate-guarding and pursuing of extra-pair females are costly in time and energy, and socially monogamous males are frequently likely to face a trade-off between the two strategies (Brodsky 1988, Hasselquist and Bensch 1991, Johnsen et al. 2003). Two common methods used by males to gain additional matings are singing (Dunn and Zann 1996, Grafe and Bitz 2004) and territorial intrusion (Stutchbury 1998, Komdeur et al. 1999, Double and Cockburn 2000, Mays and Ritchison 2004). These are more likely to be used by territorial, strong-flying species where males maintain relatively large spatial separation from potential extra-pair females. For Tibetan Eared-pheasants, mate-guarding was highly effective and reduced the probability of attracting additional females. Male-male lateral display seemed to be a better resolution to the conflict of interest in a social environment in which synchronously breeding non-territorial males met frequently. When on the receiving end of a display, lower-ranking male Tibetan Eared-pheasants did not leave their mates even though they had the risk of having their status reduced. The presence of these males, as demonstrated in other birds (Møller 1987, Westneat 1993, Pinxten and Eens 1997), could act as a potential deterrent to higher-ranking opponents. In territorial birds, territory owners usually win over conspecific intruders, illustrating an advantage of prior residence (Cristol et al. 1990, Wiley 1990). For Tibetan Eared-pheasants, male possession of a mate should equate with prior residence, which could restrict higher-ranking males from converting their displays into an attack to obtain extra-pair copulations.

My observations show that male Tibetan Eared-pheasants have developed adaptive behaviors to handle the conflict between gregariousness resulting from limited space and maintaining monogamy, and the conflict between mate-guarding and pursuing extra-pair fertilizations. These adaptations were reached by forming linear dominance, displaying to lower-ranking rivals to attract additional females, remaining vigilant to detect extra-mating attempts of other males, and evading higher-ranking rivals to reduce potential opportunities of paternity loss.

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NATURAL HISTORY AND POPULATION STATUS OF THE YELLOW-SHOULDERED PARROT ON LA BLANQUILLA ISLAND, VENEZUELA

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ABSTRACT.—The Yellow-shouldered Parrot (*Amazona barbadensis*) has a disjunct geographical distribution and the smallest population of the species inhabits La Blanquilla Island in the southern part of the Caribbean Sea. We conducted field work from 1993 to 1998 to gather information on the natural history and population status of this parrot on La Blanquilla. We compared that information with similar data gathered previously from Margarita Island. We found three communal roosts on La Blanquilla and estimated the parrot population to be ~100 individuals. We found an average of 8.8 ± 3.6 active nests/year; all nests were in the central and western parts of the island, mainly in tree cavities of *Guaiacum officinale*. Nests on La Blanquilla Island were closer to the ground than nests on Margarita Island. The breeding season on La Blanquilla Island started later and clutch size was lower (2.24 ± 0.95 eggs/nest) than on Margarita Island. Parrots were observed foraging on 12 plant species; most observations involved consumption of the fruit of *Casearia tremula* (Flacourtiaceae). The main threats to Yellow-shouldered Parrots on La Blanquilla are predation and illegal poaching. Survival of the Yellow-shouldered Parrot on La Blanquilla Island is uncertain because of small population size and increasing threat levels. *Received 6 March 2006. Accepted 27 January 2007.*

The Yellow-shouldered Parrot (*Amazona barbadensis*) is one of the most endangered parrot species in Venezuela as a consequence of illegal pet trade and habitat loss (Desenne and Strahl 1991, Collar et al. 1994, Rodríguez and Rojas-Suárez 1995). Its total population size is estimated at 10,000 individuals and it is considered vulnerable at a global level (BirdLife International 2000). This species is patchily distributed throughout the arid zones of the Venezuelan northern coast, and on the Caribbean islands of Bonaire (Netherlands Antilles), Margarita, and La Blanquilla (Forshaw 1989, Collar et al. 1994, Juniper and Parr 1998). The Yellow-shouldered Parrot became extinct on Aruba during the 1950's (Forshaw 1989) and probably also disappeared from Curaçao (Juniper and Parr 1998).

Populations living on islands are often more vulnerable to extinction than mainland counterparts (MacArthur and Wilson 1967, Soulé 1987, Whittaker 1998); thus, monitoring the conservation status of the three remaining island populations of the Yellow-shouldered Parrot is a priority goal. A conservation program for the Yellow-shouldered Parrot has been conducted on Margarita Island by a Venezuelan NGO (PROVITA) since 1989. The present program includes research, monitoring, management, and public awareness and educational campaigns (Albornoz et al. 1994).

The smallest island inhabited by the Yellow-shouldered Parrot is the Venezuelan island of La Blanquilla (64.5 km^2) in the southern part of the Caribbean Sea. The first records of this parrot on La Blanquilla were by the British zoologist P. R. Lowe, who visited the island in 1906. He reported this species was common and that large flocks were observed at evening (Lowe 1907). Phelps (1947) observed Yellow-shouldered Parrots in the same areas where Lowe had found them and reported that he observed no parrots in the central region of the island. Forshaw (1989) highlighted the lack of information on Yellow-shouldered Parrots living on La Blanquilla after Lowe's reports. A preliminary evaluation of the status of the Yellow-shouldered Parrot on La Blanquilla was conducted in 1992 (Rojas-Suárez 1994a). That visit was followed by subsequent trips by PROVITA's staff from 1993 to 1998. The results of those trips are presented here. Our objective was to gather information on the natural history (i.e., breeding, foraging, and location of communal

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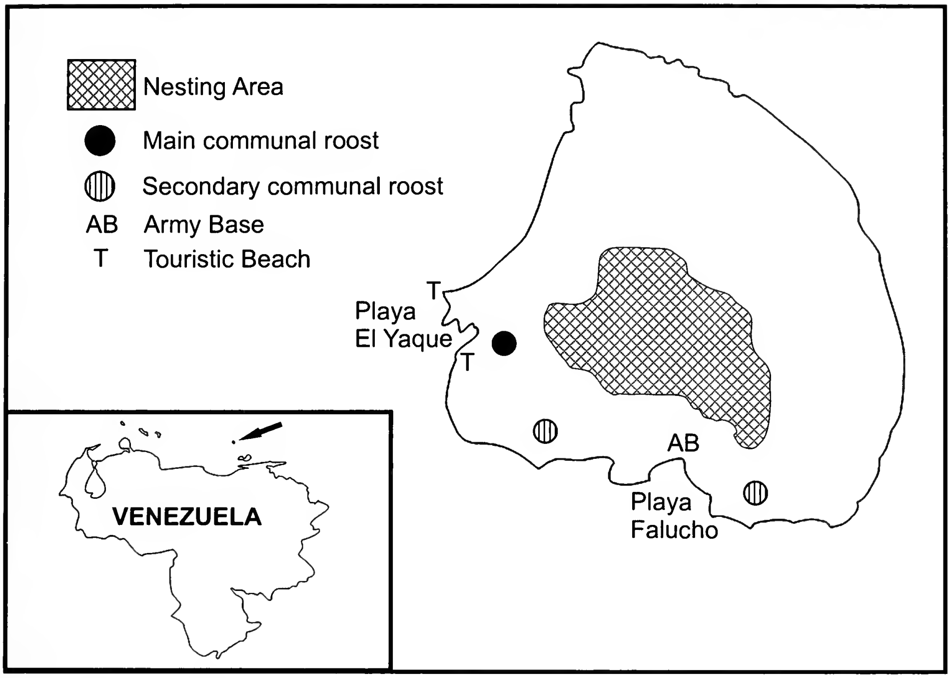

FIG. 1. La Blanquilla Island, showing important sites for Yellow-shouldered Parrots.

roosts) and population status of the Yellow-shouldered Parrot on La Blanquilla Island to provide baseline data for design of conservation and management strategies for this species. We also compare characteristics of the parrot populations inhabiting Margarita and La Blanquilla islands.

METHODS

Study Area.—La Blanquilla (11° 51′ N, 64° 36′ W) is an emerged island in the southern Caribbean Sea, 90 km northeast of Margarita Island, and 170 km northeast of Venezuela's mainland (Fig. 1) (Williams Trujillo 1980). It is small (64.5 km^2) with a maximum width of 11 km, a total coastline of ~25 km, and a maximum elevation of 30 m above sea level (Cervigón 2001). The average annual temperature is 25 °C, and annual rainfall ranges from 300 to 600 mm (Williams Trujillo 1980). Most of the island is covered by xerophytic vegetation, including dense cacti formations dominated by *Opuntia wentiana* and *O. caribea*. Columnar cacti, such as *Stenocereus griseus*, also are common in some areas. Vegetation in the central portion of the island includes scattered trees (*Guaiacum officinal*e, *Capparis odoratissima*, *Pithecellobium ungis-cati*, and *Ficus britonni*), whereas coastal vegetation is dominated by mangrove (*Conocarpus erectus*) (Williams Trujillo 1980).

There is no stable human population on La Blanquilla but fishermen coming from Margarita Island at times stay on the southern and western coasts of the island for several months each year (Cervigón 2001). The Venezuelan army established a Coastal Guard Station (Estación Secundaria de Guardacostas) on La Blanquilla in 1986 at which now reside 30–35 officials and sailors. Small groups of tourists (20–25 people) made single-day visits to the island from 1994 to 2000 but their activities were restricted to two beaches on the western coast.

Roosting Sites and Estimation of Population Size.—Our field work was conducted from 1993 to 1998. We conducted one 4-day field trip in October 1993, two 1-week field trips in 1994 (Jul, Aug) and 1995 (Jun, Aug) with 1-week field trips in August 1996, August 1997, and July 1998. We used two approaches to locate communal roots. During each trip we made daily searches of vegetation patches that included large trees in different areas of the island; searches were conducted from 1600 to 1900 hrs. We also followed parrot flocks observed flying in consistent directions. We conducted simultaneous surveys at 2–3 communal roosts during 3 consecutive days from 1600 to 1900 hrs and recorded the number of parrots arriving at the roosting site during each survey following Gnam and Burchsted (1991). We compensated for movements among parrots to avoid multiple counts of the same individuals by subtracting the number of individuals flying from communal roosts.

Reproduction.—We conducted systematic searches every day from 0600 to 1500 hrs during every trip in the central part of the island where most large trees are located. We checked trees with natural cavities including former nest sites to find active nests. Each cavity was inspected with a small flashlight and a mirror, and was considered active if we found an incubating female, eggs, or chicks. We recorded egg and chick status (i.e., number, age), and estimated the mean clutch size per year. We made a series of measurements to describe cavities for each new active nest found: tree diameter at breast height, entrance horizontal width, entrance vertical width, entrance height from ground to lower edge, cavity depth, horizontal cavity diameter, and transversal cavity diameter, which is the diameter crosswise to the direction from the entrance.

Foraging.—We recorded all observations of parrots feeding during all field trips as a single foraging event, regardless of the number of parrots involved. We recorded the location where parrots were foraging, as well as the plant species and parts of the plant consumed (e.g., fruit, seed).

Identification of Threats.—We recorded signs of depredation (e.g., predator tracks) and poaching (e.g., human tracks and absence of nestlings, branches or crotches cut from a tree and placed against the tree trunk to assist in climbing, or trees with machete or axe cuts near the cavity). We also collected information on the extent of poaching through interviews with fishermen and sailors living on La Blanquilla during the breeding season.

Statistical Analyses.—Descriptive statistics represent averages ± SD. We used seven independent nonparametric analyses of variance (Kruskal-Wallis tests) to examine whether average clutch size and average values for cavity dimensions of nests varied between Yellow-shouldered Parrot populations inhabiting La Blanquilla and Margarita islands. All statistical analyses were conducted using SPSS 13.0 (SPSS Institute, Inc. 2004) with significance accepted at $P < 0.05$ for clutch size comparisons. The significance level for cavity comparisons was set at $P < 0.007$ after a Bonferroni correction.

RESULTS

Roosting Sites and Estimation of Population Size.—No communal roosts were found during 1993 and 1994, and small parrot flocks were observed flying in different directions during the evenings. We found two roosting sites in 1995: one in the southern part of the island, west of Playa Falucho, where 13 parrots spent the night together, and the main communal roost with about 40 parrots, in the southwestern portion of the island close to Playa El Yaque (Fig. 1). Parrots congregated at three communal roosts in 1996 including the same two sites of the previous year and at another one south of the main roosting site, where ~20 individuals arrived every evening. These same three roosting sites were visited by parrots every evening during 1997 and 1998. The roost near Playa El Yaque was the largest and a maximum of 62 parrots was recorded there at one time. We counted a maximum of 14 and 21 parrots, respectively, at the two secondary roosts. We estimated the population size of the Yellow-shouldered Parrot on La Blanquilla Island at ~100 individuals based on the maximum estimated number for a single day in a given year.

Reproduction.—We checked an average of 83.4 ± 12.2 cavities/year (range = 68–95) and found an average of 8.8 ± 3.6 active nests/year (range = 4–12). All active nests were in the central and western parts of the island (Fig. 1). We located 44 active nests during 1993–98. All but one were in secondary cavities of *Guaiacum officinale*. One nest was in a cavity of an unidentified tree known as "Palo Blanco" by local fishermen. The average cavity dimensions for the active nests on La Blanquilla Island varied (Table 1). The only significant difference in cavity dimensions between Margarita and La Blanquilla is-

TABLE 1. Cavity dimensions for nests of the Yellow-shouldered Parrot on La Blanquilla and Margarita islands, Venezuela.

	La Blanquilla			Margarita		
Measurement (cm)	Mean ± SD	Range	*n*	Mean ± SD	Range	*n*
Tree diameter at breast height	169.0 ± 61.3	90–276	14	156.9 ± 49.5	35–303	115
Entrance horizontal width	13.1 ± 5.8	6–30	15	12.5 ± 5.5	5–50	116
Entrance vertical width	20.4 ± 14.7	10–67	15	27.5 ± 22.2	7–154	114
Entrance height from ground	149.9 ± 55.4	30–240	15	273.0 ± 160.0	40–893	115
Horizontal cavity diameter	30.2 ± 22.6	7–95	13	22.5 ± 12.2	5–94	114
Transversal cavity diameter	73.0 ± 39.1	21–106	4	37.9 ± 27.0	10–140	90
Cavity depth	73.7 ± 24.6	41–126	15	89.4 ± 58.0	4–320	114

lands was the entrance height from ground ($H = -3.43$, $P < 0.001$); nests on La Blanquilla Island were closer to the ground than nests on Margarita Island (Table 1).

We estimated the breeding season on La Blanquilla Island, based on age of clutches in nests, begins in mid-May to early June and extends to late August or early September. Clutch size during our study was 2.24 ± 0.95 eggs/nest with a range of 1 to 4 and a mode of 2 eggs (Table 2). Clutch size was similar across years but differed ($H = -5.23$, $P < 0.001$) from that reported earlier on Margarita Island (3.38 ± 0.78 eggs/nest, $n = 322$, range = 1–5, mode = 4 eggs).

Foraging.—We observed parrots foraging in the central, southwestern, and western portions of the island. Yellow-shouldered Parrots fed on 16 different items of 12 plant species belonging to 10 families (Table 3). From pooled observations from all years ($n = 48$), fruits of *Casearia tremula* (Flacourtiaceae) were most frequently consumed (33.3%). Nestlings were mainly fed fruits of *Casearia tremula* and *Stenocereus griseus.*

Threats.—The main threats to Yellow-shouldered Parrots on La Blanquilla are predation by introduced species (there are no natural predators) and poaching. Populations of introduced species, such as domestic cats (*Felis catus*) and Norway rats (*Rattus norvegicus*) appear to have increased in the last decade. Cats were observed frequently throughout the island during all field work. We observed a cat sleeping inside a cavity in 1997 and, that same year, a cat's skull was found within another cavity. We also found marks of cat's claws at the entrance of some cavities. Rats and their nest materials were also frequently found inside some cavities.

TABLE 2. Clutch size of the Yellow-shouldered Parrot on La Blanquilla Island, Venezuela, 1994–1998.

Year	Mean ± SD	Range	*n*
1994	2.11 ± 1.17	1–4	9
1995	2.60 ± 0.97	1–4	10
1996	1.67 ± 0.58	1–2	3
1997	2.33 ± 0.58	2–3	3
1998	2.10 ± 0.74	1–3	4
1994–98	2.24 ± 0.95	1–4	29

An important threat to Yellow-shouldered Parrots on La Blanquilla Island appears to be poaching by fishermen who visit the island for short periods. We estimated that poachers harvested 75% of the nests in 1996, because we found three active nests and nine additional cavities with recent signs of parrot activity (e.g., feathers, egg shells) but without nestlings at a time of the year that was too early for the chicks to have fledged. Cavities in four of these nine trees had obviously been chopped open, evidently to remove chicks; these cavities were not used subsequently for nesting.

DISCUSSION

The population of Yellow-shouldered Parrots on La Blanquilla is particularly interesting from a conservation perspective. Its current population size is small (90–100 individuals), which makes it highly susceptible to extinction (Rodríguez et al. 2004). It is important to emphasize that our surveys were conducted during the final part of the breeding season when females are no longer staying in nests at night (Sanz and Rodríguez-Ferraro 2006). Thus, it is unlikely that we underesti-

TABLE 3. Plant species and items consumed by the Yellow-shouldered Parrot on La Blanquilla Island, 1993–1998.

Family	Species	Item eaten
Boraginaceae	*Bourreria cumanensis*	Fruit
Cactaceae	*Stenocereus griseus*	Fruit, branch tip
Capparidaceae	*Capparis odoratissima*	Fruit, flower bud
Flacourtiaceae	*Casearia tremula*	Fruit, seed
Poaceae	*Cenchrus* sp.	Seed
Leguminosae	*Tamarindus indica*[a]	Fruit, flower
	Pithecellobium ungis-cati	Seed
	Prosopis juliflora	Seed
Moraceae	*Ficus britonni*	Fruit
Arecaceae	*Cocos nucifera*[a]	Flower bud
Theophrastaceae	*Jacquinia revoluta*	Fruit
Zygophyllaceae	*Guaiacum officinale*	Fruit

[a] Introduced plants.

mated population size because of the time of the year when we conducted the surveys. We were not able to ascertain whether the parrot population was declining because our population size estimates were similar over the entire period. Additional limitations included the difficulty we had finding communal roosts during the first years of this study, and the impossibility of conducting simultaneous surveys at more than two sites during some trips. These limitations can result in an underestimation of population size. When we compared our population-size estimates with those of previous reports, however, the population appeared to be stable. A population of 100 parrots was estimated during 1988 (Desenne and Strahl 1991) and 80 individuals were estimated in 1992. The latter was based on censuses conducted from vehicles, which allowed survey of the entire island (Rojas-Suárez 1994a).

The breeding parrot population on La Blanquilla Island is small, based on the number of active nests found each year. We are aware that we could have underestimated the total number of active nests per year because our trips were not at the beginning of the breeding season and we could miss nests that failed before our arrival on the island. This underestimation should not be large, however, because we conducted exhaustive searches in every year and because the number of active nests found was consistently low each year. Additionally, Rojas-Suárez (1994a), who searched for nests at the beginning of the breeding season in 1992, only found seven active nests. Given the maximum number of active nests found in a single breeding season was 12 and the estimated population size was 100 individuals, then up to 24% of the population may breed annually. It can be argued that number of appropriate cavities could be a limiting factor considering the low number of active nests found each year but our data suggest this may not be the case. We checked between 68 and 95 cavities per year and found more than 20 that seemed suitable as parrot nests (based on measurements and location) but that have not been used by parrots.

Average clutch size was relatively constant during 1994–1998 and is the lowest reported for any species of the genus *Amazona* (Sanz and Rodríguez-Ferraro [2006] provided interspecific comparisons). Our estimate of clutch size may be low because of our late arrival in the breeding season. However, our estimates were similar among years and similar to a previous report by Rojas-Suárez (1994a) who estimated an average clutch size of 2.20 ± 0.84 eggs/nest (range = 1–3, n = 5). Additional support for this conclusion comes from our long-term study on Margarita Island where average clutch size was relatively constant over time even though factors that can affect nest survival, such as natural mortality and predation, varied across years (Sanz and Rodríguez-Ferraro 2006).

Anthropogenic factors also affect low annual recruitment of Yellow-shouldered Parrot fledglings on La Blanquilla Island. Poaching of nestlings is the main factor reducing recruitment. Interviews with fishermen and sailors living on La Blanquilla confirmed that, during the parrots' breeding season, some fishermen visited the central part of La Blanquilla before leaving the island to collect parrot nestlings to be sold on Margarita Island. The lack of control and inefficient checking of boats leaving the island by local authorities favors the illegal trade of the species.

Native snakes and mammals, which are well recognized parrot predators in the Neotropics (Snyder et al. 1987, Enkerlin-Hoeflich 1995, Martuscelli 1997, Koenig 2001, Sanz and Rodriguez-Ferraro 2006), are absent on La Blanquilla, as is the Pearly-eyed Thrasher (*Margarops fuscatus*) which has negatively affected the population of the Puerto Rican Parrot (*Amazona vitatta*) (Snyder et al. 1987). Humans are directly responsible for introductions of possible parrot predators, such as cats and rats on La Blanquilla Island. Rojas-Suárez (1994a), for example, reported a parrot killed by a cat. The cat population on La Blanquilla in 1992 was estimated to be 24. During our study period, the cat population appears to have increased because cats were frequently observed in most parts of the island. The effect of rats and cats on recruitment and reproductive success of the Yellow-shouldered Parrot has not been evaluated directly. The impact that cats can have on the parrot population may be critical because cats can climb trees and enter nest cavities. Thus, they can easily depredate both nestlings and incubating adults. Rats also can depredate bird nests, mainly those in burrows, but also those high in trees (Atkinson 1985, Fitzgerald et al. 1991) and have been reported as egg predators for the Blue-crowned Parrot (*Aratinga acuticaudata neoxena*) on Margarita Island (Rojas-Suárez 1994b). It is obvious that cats and rats can contribute considerably to population declines, and even extinction, of island bird species (Jehl and Parkes 1983, Fitzgerald 1988, Diamond 1989, Fitzgerald et al. 1991, Martínez and Curry 1996, Dowding and Murphy 2001, Nogales et al. 2003).

The parrot population on La Blanquilla differs in several aspects (i.e., breeding, diet) from the well-studied population on Margarita Island. First, the breeding season on Margarita Island begins in late March or early April and continues until late July (Rojas-Suárez 1991, Sanz and Rodríguez-Ferraro 2006). The breeding season on La Blanquilla Island occurs much later, perhaps because of drier weather. In 1998, a year of extreme drought on Margarita Island, the breeding season began in mid-May (Sanz and Rodríguez-Ferraro 2006), which indicates that rainfall patterns may influence the initiation of the breeding season.

Tree species used for nesting by Yellow-shouldered Parrots also differ between islands. Eighty-five percent of 117 nests on Margarita Island were in *Bulnesia arborea* and only 3% were in *Guaiacum officinale* (Sanz 2004). This difference may be a consequence of general vegetation differences between the two islands. Tree diversity in the Macanao Peninsula, the part of Margarita Island where parrots live, differs from that on La Blanquilla. The type of tree used by parrots also affects morphometric characteristics of nest cavities. Parrot nests in La Blanquilla were lower that those on Margarita Island, largely because *G. officinale* trees are shorter than *Bulnesia arborea* trees.

Clutch size differed between parrot populations on Margarita and La Blanquilla islands which may be a result of differences in food availability. It is widely accepted that clutch size is adapted to a limited food supply (Lack 1954, Cody 1966, Martin 1987). Even though our foraging observations are limited and cover only the breeding season, we found interesting differences in the diet of Yellow-shouldered Parrots between the two islands that may be indicative of food limitation on La Blanquilla. The main food item on this island, the fruit of *Casearia tremula*, is consumed less by parrots on Margarita Island (7% of the total foraging observations, $n = 491$, unpubl. data), where the main food during the breeding season is fruit of the columnar cactus *Stenocereus griseus* (Silvius 1995, Stolk 1997). Some items consumed on Margarita Island, such as fruits of *Castella erecta*, were available on La Blanquilla, but we did not observe parrots eating them. Conversely, we recorded food items at La Blanquilla that were not reported as being used by parrots on Margarita Island, such as seeds from the grass *Cenchrus* sp., which parrots ate on the ground, a foraging behavior seldom exhibited by this species.

The survival of the Yellow-shouldered Parrot on La Blanquilla Island is uncertain because of its small population size and current threat levels. Additional studies, especially on recruitment, are needed to fully understand the population dynamics of the species on La Blanquilla Island.

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BIRDS OF AN OPEN VEGETATION ENCLAVE IN SOUTHERN BRAZILIAN AMAZONIA

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ABSTRACT.—We report on the ornithological results of the first rapid biodiversity survey in the BX-044 polygon, one of the largest open vegetation enclaves in southern Amazonia, in the Brazilian states of Amazonas and Rondônia. Three-hundred and thirty species were recorded in all habitats surveyed, including closed (*terra-firme,* riparian, gallery, and *campinarana* forests) and open (*cerrado* and grassland) vegetation types. Over 90% (298) of all species were not shared between closed and open habitat types emphasizing the importance of inter-habitat diversity to the overall species richness recorded. Significant range extensions were documented for 34 species (30 of which were associated with the *cerrado* biome). Open vegetation enclaves contribute significantly to local avian species richness in Amazonia in addition to supporting species with special relevance to conservation with ranges centered in the *cerrado,* currently one of the most threatened biomes of South America. Conservation of Amazonian *cerrado* enclaves offers the unique opportunity to combine preservation of areas with high inter-habitat diversity with establishment of a complementary network of conservation units directed at preserving the *cerrado* biome throughout South America. Urgent steps must be taken to protect Amazonian open vegetation enclaves, which are still conspicuously under represented in the network of Brazilian conservation units, despite the fairly recent expansion of agriculture into these areas. *Received 28 October 2006. Accepted 5 March 2007.*

The bird fauna of the Amazon Basin consists mostly of species associated with tall seasonally flooded and non-flooded humid forests (Haffer 1978, Remsen and Parker 1983). Despite their smaller contribution to the total regional species richness, isolated patches of non-forest vegetation in Amazonia contain a distinct avifauna with obvious closer biogeographic affinities to the avifauna of other non-forest biomes in the Neotropics (Haffer 1985, Silva 1995a). The non-forest vegetation of the Amazonian lowlands is distributed locally throughout the region occurring as isolated patches of different sizes in a matrix of forest habitats (Capobianco et al. 2001, Silva and Bates 2002). The two main non-forest vegetation types occurring in Amazonia are the savannas (*cerrado*; Eiten 1972), and sandy-soil fields and scrubs (*campina*; Anderson 1981). The transition between those habitats and the surrounding rain forest is usually smooth with recognition of several intermediate physiognomies such as tall savanna (*cerradão*) and white sand forest (*campinarana*; Capobianco et al. 2001).

The comparatively small number of studies focusing on the non-forest avifauna of the Amazon Basin (Henriques and Oren 1997, Silva et al. 1997, Sanaiotti and Cintra 2001), coupled with the widespread conversion of open habitats into crop fields currently occurring at an alarming rate in southern Brazilian Amazonia (Morton et al. 2006), indicate the urgent need for additional biodiversity surveys of areas covered by open and semi-open habitats in this region. These surveys have been recognized by the Brazilian government and scientific community as key to the effort of improving knowledge of the composition of animal and plant communities across Amazonia to update biodiversity data needed to identify conservation priorities in this region (Capobianco et al. 2001).

We report the ornithological results of the first biodiversity survey to occur in one of the largest patches of savanna in southern Brazilian Amazonia: the upper Marmelos River region (included in the BX-044 polygon; Capobianco et al. 2001), which is on the "arc of deforestation" near the borders of the states of Amazonas, Mato Grosso, and Rondônia (Fearnside 2005).

METHODS

We surveyed different localities between 24 October and 17 November 2003 within the BX-044 polygon, one of the largest open veg-

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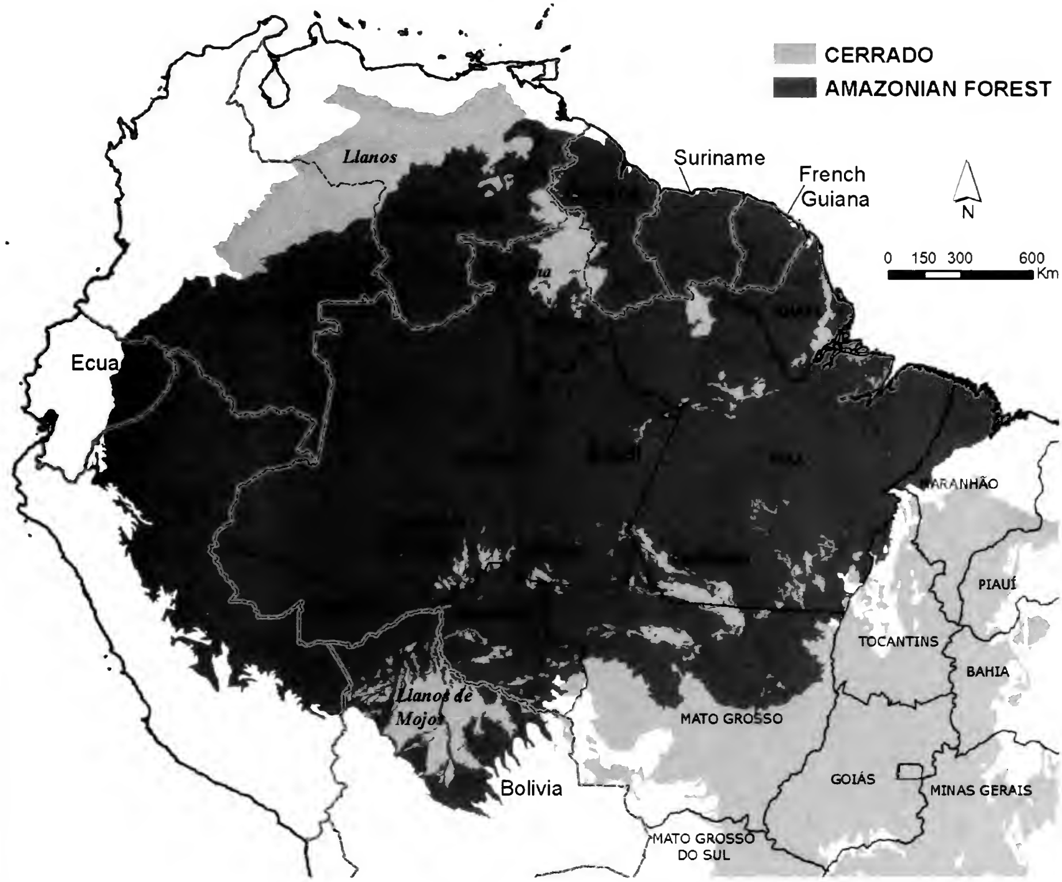

FIG. 1. Distribution and size of the main Amazonian *cerrado* enclaves, including the BX-044 polygon. The largest southern (Llanos de Mojos, Campos de Humaitá and Serra do Cachimbo) and northern (Roraima) Amazonian *cerrado* enclaves are identified.

etation enclaves in Amazonia (Fig. 1). Prior to our study, the BX-044 polygon was officially recognized as a first-order priority site for future biodiversity surveys and conservation in Brazilian Amazonia (Capobianco et al. 2001). The BX-044 polygon is in the territories of four different municipalities in the states of Amazonas and Rondônia. However, all localities sampled were within the municipality of Manicoré, State of Amazonas, ~280 km south of Manicoré City.

The habitat in the BX-044 polygon is a complex mosaic including *terra-firme* (upland) forest, *campinarana* (sandy-soil low canopy forest), and more open vegetation types such as *cerrado* (savanna), *campina* (sandy-soil scrub), and undisturbed grassland (Fig. 2). We designed our survey to maximize the coverage of these major habitats and used a remote sensing analysis to map the location of each major vegetation type (M. P. C. Schneider, unpubl. data).

Birds were observed with binoculars and tape recorded with a Sony TCM 5000 cassette recorder and a Sennheiser ME66 microphone in all localities surveyed. Voucher specimens were collected and deposited in the ornithological collection of the Museu Paraense Emílio Goeldi (hereafter MPEG) in Belém, State of Pará, Brazil.

We tried to distribute our sampling effort among the different habitats according to their proportional coverage of the BX-044 polygon. The following sampling effort (number of hours) was expended by AA while observing, tape-recording, and collecting birds in the dif-

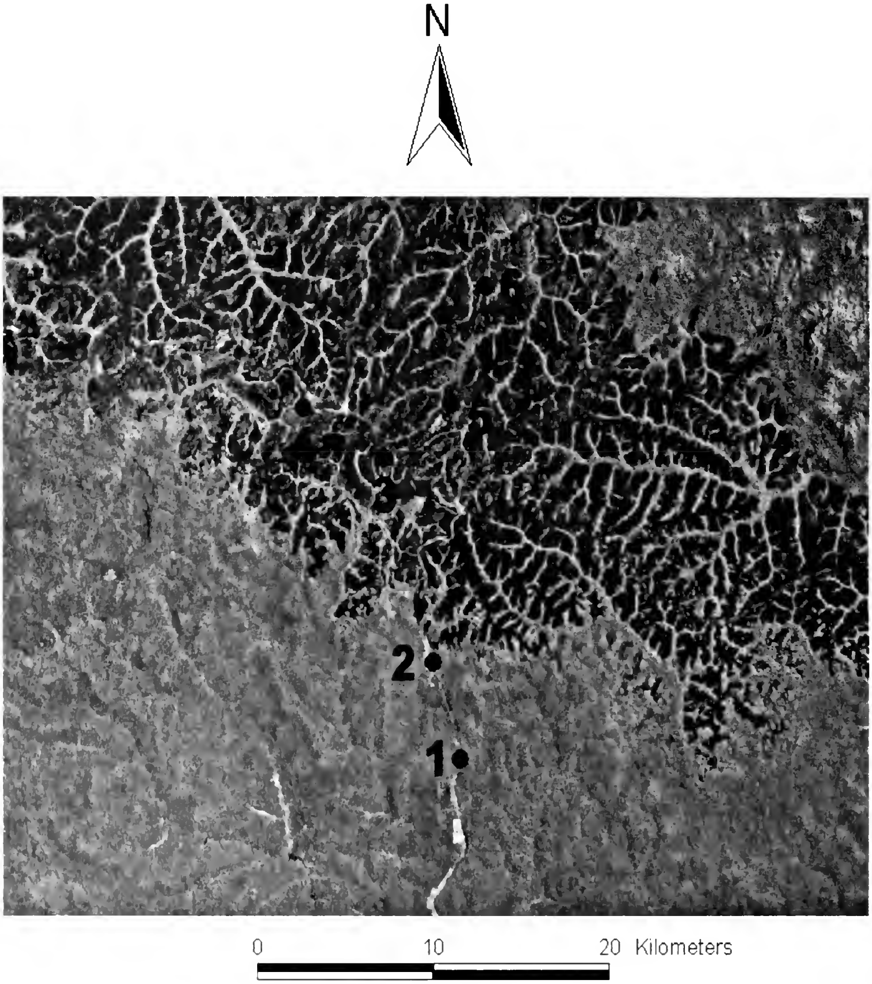

FIG. 2. Satellite image showing the forest–*cerrado* ecotone at the BX-044 polygon surveyed in October–November 2003. Darker colors denote areas covered by open vegetation (*campina, cerrado,* and grassland), while light colors indicate areas covered by forest (riparian forest, gallery forest, *terra-firme,* and *campinarana*). Localities 1, 2, 3, and 4 are along a dirt road across the BX-044 polygon. Locality 1 = KM 137—"Km 137 of Rodovia do Estanho" (8° 41′ S, 61° 24′ W) sampled between 24 October and 1 November, and covered primarily by upland *terra-firme* forest on sandy-soils. Locality 2 = KM 126—"Km 126 of Rodovia do Estanho" (8° 39′ S, 61° 25′ W) sampled between 2 and 7 November and covered by a mosaic of riparian forest, *campinarana* (sandy-soil low canopy forest), unclassified transitional physiognomies, and man-made disturbed habitats. Locality 3 = FPF—"Fazenda Passo Formoso" (8° 33′ S, 61° 26′ W) surveyed between 8 and 17 November and covered by gallery forest, *cerrado,* and grassland. Locality 4 = FCA—"Fazenda Campo Alegre" (08° 31′ S, 61° 29′ W) surveyed between 8 and 17 November and covered by grassland and *cerrado.* Locality 5 = FBV–"Fazenda Bela Vista" (8° 31′ S, 61° 24′ W) surveyed between 8 and 17 November and covered by gallery forest, grassland, and *cerrado.* Locality 6 = FC–"Fazenda Copeares" (8° 28′ S, 61° 23′ W) surveyed between 8 and 17 November and covered by gallery forest and *cerrado.*

ferent vegetation types surveyed: *terra-firme* forest (63), riparian forest (21), gallery forest (4), campinarana (28), cerrado (40), and grassland (38). Mist nets were operated independently by FP and D. C. P. Neto and resulted in accumulation of additional sampling effort (expressed as the number of nets used multiplied by the number of hours they stayed open): *terra-firme* forest (500), riparian forest (200), gallery forest (400), and *campinarana*

(200). Attempts to capture birds with mist nets in open *cerrado* and grassland were not overly successful, probably due to the more open characteristic of these habitats which favors visual detection. Thus, *cerrado* and grasslands were not systematically sampled with mist nets.

RESULTS AND DISCUSSION

Species Richness and Composition.—We recorded 330 bird species in all habitats surveyed (Appendix). More species (58.7% [194]) recorded during the survey were restricted to predominantly forested habitats (*terra-firme* forest, riparian forest, gallery forest, and *campinarana*) whereas 31.5% (104) occurred only in open and semi-open habitats (*cerrado,* grassland, and man-disturbed areas).

It is not surprising that nearly a third of all species recorded in the BX-044 polygon were in association with open vegetation types, especially *cerrado.* Of the 34 species for which significant range extensions were documented in the BX-044 polygon, 30 (88%) were typical *cerrado* species (Silva 1995b). Few southern Amazonian open vegetation enclaves have been sampled by ornithologists; published avifaunal surveys are available for several southern Amazonian *cerrado* enclaves: Llanos de Mojos in Bolivia (Gyldenstolpe 1945), Pampas del Heath in Peru (Graham et al. 1980), and Humaitá (Hellmayr 1910), Alter do Chão (Sanaiotti and Cintra 2001), and Serra do Cachimbo (Pinto and Camargo 1957) in Brazil. These surveys and the present study show that many species associated with nonforest habitats in the *cerrado* region of central South America (Silva 1995b) occur well inside the Amazonian biome. The extent to which avian species richness and composition correlate with *cerrado* enclave size and distance from the continuous *cerrado* biome in central South America remains to be assessed.

Noteworthy Records.—We recorded 34 species in the BX-044 polygon for which the southeastern corner of the State of Amazonas represented a major range extension including some locally distributed, poorly known, and rare species.

White-tailed Kite—*Elanus leucurus.* One individual was observed on 12 November 2003 hovering in search of prey over an open natural grassy field with scattered patches of *cerrado* at Fazenda Bela Vista (FBV). This species is distributed locally in Amazonia (Haverschmidt and Mees 1994, Henriques and Oren 1997, Sick 1997), mostly in isolated patches of savanna. The timing of our record (mid-Nov) suggests that a resident and possibly breeding population of this species may occur in Brazilian Amazonia.

White-tailed Hawk—*Buteo albicaudatus.* One but possibly two adults were observed on 9 and 15 November 2003 at FBV. The first observation consisted of a perched individual on the ground in a recently grazed crop field. The second record was of an individual observed soaring over a natural grassy field with scattered patches of *cerrado,* a few kilometers from the location of the first record. The few available records in Brazilian Amazonia of this locally distributed species are from open areas in the states of Amapá (Novaes 1974), Amazonas (e.g., Manaus eastward; Thiollay 1994, Cohn-Haft et al. 1997), Pará (e.g., Marajó Island; Henriques and Oren 1997), and Roraima (Pinto 1966).

Long-tailed Ground-dove—*Uropelia campestris.* Two males (MPEG 57507 and 57509) and one female (MPEG 57508) of this small dove were observed and collected on 11 November 2003 in an open disturbed grassy field with scattered low bushes at Fazenda Passo Formoso (FPF). Previous records of this species for Amazonia are from wet and upland natural fields in: (1) the southeastern State of Pará along the Araguaia River Valley (locality of Santana do Araguaia; 9° 50′ S, 50° 15′ W; specimens MPEG 48503 and 48504 collected by D. C. Oren, D. P. Neto, and M. S. Brígida on 8 Aug 1992); (2) Marajó Island, State of Pará (Henriques and Oren 1997); and (3) State of Amapá (Silva et al. 1997). Our record represents the first for the Brazilian State of Amazonas and significantly extends the range of this species northwest. The nearest locality where the Long-tailed Ground-dove has been reported is in the State of Mato Grosso, near the *cerrado*–rainforest ecotone, >750 km south of the BX-044 polygon (Silveira and D'Horta 2002).

Yellow-chevroned Parakeet—*Brotogeris chiriri.* Several flocks of this parakeet were seen and heard flying over *cerrado* and grassy fields between 10 and 17 November 2003 at FBV and Fazenda Copeares (FC). A small group of six individuals was tape-recorded on 14 November while perching in the canopy of gallery forest edge at FC. The Yellow-chevroned Parakeet is distributed predominantly in the *cerrados* of central South America, reaching the savanna–Amazonian forest ecotone in the Brazilian states of Mato Grosso and Pará (Collar 1997). One apparently isolated population has been recorded at Serra do Cachimbo (Pinto and Camargo 1957; MPEG 22070), another large Amazonian *cerrado* enclave east of the BX-044 polygon (Fig. 1). Our record is the second for the Yellow-chevroned Parakeet in Amazonia and the first for the Brazilian State of Amazonas. Amazonian populations of the Yellow-chevroned Parakeet have had an important role in the definition of species limits within the *Brotogeris versicolurus* (Canary-winged Parakeet)/*chiriri* species complex, which have alternately been treated as conspecific (Meyer de Schauensee 1970), or separate species (Remsen et al. 2006). Pinto and Camargo (1957) remarked that specimens collected at Serra do Cachimbo showed no signs of phenotypic intergradation with the Canary-winged Parakeet, an exclusive Amazonian species. This comment has been widely misinterpreted as a report of sympatry without interbreeding between *B. versicolurus* and *B. chiriri* (e.g., Collar 1997). However, there have been no confirmed reports of sympatry between these two taxa. The Canary-winged Parakeet occurs in seasonally flooded forest (*várzea*) and disturbed habitats along the entire Amazon/Solimões River Valley in Peru, Colombia, Brazil, and along the coast of the Brazilian State of Amapá and French Guyana. The Yellow-chevroned Parakeet is associated with *cerrado* and gallery forest patches in open vegetation enclaves in southern Brazilian Amazonia (Collar 1997; MPEG specimens).

Burrowing Owl—*Athene cunicularia.* A single pair of this species was continuously observed in a disturbed pasture at FPF between 8 and 17 November 2003. The Burrowing Owl is largely absent from the Amazon Basin despite its widespread distribution throughout the Americas (Marks et al. 1999). This species in Brazilian Amazonia has been recorded in *cerrado* and extensive cleared forest patches in Amazonas (Cohn-Haft et al. 1997), Mato Grosso (Zimmer et al. 1997), Pará (specimen MPEG 48527 collected at Santana do Araguaia by D. C. Oren, D. P. Neto, and M. S. Brígida on 8 Aug 1992), and Roraima (Pinto 1966). Records from the central part of the State of Amazonas (Cohn-Haft et al. 1997) and northern part of the State of Mato Grosso (Zimmer et al. 1997) seem to indicate the Burrowing Owl is expanding its distribution throughout Amazonia following extensive forest conversion into pastures and crop fields.

Least Nighthawk—*Chordeiles pusillus.* An adult male of this species was collected on 13 November 2003 in slightly disturbed open *cerrado* with scattered low trees at Fazenda Campo Alegre (FCA) (MPEG 57529). The Least Nighthawk in Amazonia is confined to patches of savanna and shrubby *campina* in Guyana (Braun et al. 2000), Venezuela (Hilty 2003), and Colombia (Hilty and Brown 1986). In Brazilian Amazonia, it has been recorded in the states of Amapá (Novaes 1974, Silva et al. 1997), Amazonas (at Jaú National Park; Borges et al. 2001), Mato Grosso (Novaes and Lima 1991), Pará (Pinto and Camargo 1957, Dickerman 1988, Henriques and Oren 1997), and Roraima (Pinto 1966). The specimen collected in the BX-044 polygon fits the description of subspecies *saturatus* from the southwestern part of the State of Pará (Serra do Cachimbo; Pinto and Camargo 1957) and northern Mato Grosso (Novaes and Lima 1991). It is separated from the remaining, mostly northern Amazonian populations (*septentrionalis* and *esmeraldae*), by a darker sooty overall color and wider black bars on the lower chest, belly, and undertail coverts. Dickerman (1988), who did not read the original description of *saturatus* in Portuguese, mistakenly reported *saturatus* as having white instead of barred undertail coverts. A second specimen of the Least Nighthawk was collected by D. C. P. Neto (MPEG 46462; unknown gender) on 7 November 1991 ~200 km west of the BX-044 polygon near the city of Humaitá (on the left bank of the Madeira River at 7° 31′ S, 63° 02′ W; coordinates obtained from Paynter and Traylor 1991) in the Humaitá *cerrado* enclave (Fig. 1). This specimen differs significantly from our specimen collected in the BX-044 polygon and suggests that at least two different taxa of the Least Nighthawk are separated by the upper Madeira River.

Cinnamon-throated Hermit—*Phaethornis nattereri*. One unknown gender individual and a female of this species were netted and collected on 11 and 12 November 2003 on the edge of gallery forest at FBV (MPEG 57538–57539). No other individuals were recorded in the BX-044 polygon during the entire survey, possibly due to our restricted sampling of the gallery forest habitat. The Cinnamon-throated Hermit, prior to our record, was known to occur in *cerrado* and dry forest patches in eastern Bolivia, and the Brazilian states of Mato Grosso, Mato Grosso do Sul, Goiás, Tocantins, Maranhão, Piauí, and Ceará (Hinkelmann 1988, Bates et al. 1989, Schuchmann et al. 1999); in Maranhão and Mato Grosso, it has been recorded in the *cerrado*–rainforest and dry forest–rainforest ecotones (Grantsau 1968, Silveira and D'Horta 2002). Historical records of the Cinnamon-throated Hermit for some open vegetation enclaves along the lower Amazon River Valley have been regarded as doubtful, but our record from the BX-044 polygon confirms this species inhabits *cerrado* enclaves in Amazonia (Hinkelmann 1988, Schuchmann et al. 1999). The nearest record of the Cinnamon-throated Hermit to the BX-044 polygon (~350 km to the south) consists of a series of five specimens collected in *cerrado* by J. C. Roma and M. S. Brígida between 13 and 23 May 2002 near Pimenta Bueno (11° 44′ S, 60° 43′ W and 11° 45′ S, 61° 02′ W), State of Rondônia, and currently deposited at the bird collection of Universidade de Brasília, Distrito Federal, Brazil (COMB 2219–2223).

Planalto Hermit—*Phaethornis pretrei*. A few individuals of the Planalto Hermit were heard and seen in open wet grassland and *cerrado* between 8 and 16 November 2003 at FBV. The Planalto Hermit is widely distributed south of the Amazon River in open landscapes of central and eastern South America (Schuchmann et al. 1999), and our record seems to be the first for the Amazon Basin apart from four specimens collected by a MPEG ornithological expedition at Amarante do Maranhão (4° 91′ S, 47° 24′ W), State of Maranhão in extreme eastern Amazonia (MPEG 37668, 37841, 40823, and 40824) in 1986 and 1987. The nearest locality to the BX-044 polygon where the Planalto Hermit has been recorded is the upper Guaporé River Valley on the *cerrado*–Amazonian forest ecotone, in the State of Mato Grosso (Schuchmann et al. 1999) ~800 km south.

Green-tailed Goldenthroat—*Polytmus theresiae*. An unknown gender individual of Green-tailed Goldenthroat (MPEG 57546) was tape-recorded and collected on 15 November 2003 in open *cerrado* at FC. This species is associated with patches of *cerrado* and shrubby *campina* throughout Amazonia with most records from sites north of the Amazon/Solimões/Ucayali River (Novaes 1974, Cohn-Haft et al. 1997, Borges et al. 2001, Alvarez 2002). The Green-tailed Goldenthroat south of this river has been recorded mostly east of the Tapajós River (Oren and Parker 1997, Novaes and Lima 1998, Sanaiotti and Cintra 2001) in eastern Amazonia with a single record for the Purus River drainage in southwestern Amazonia (Gyldenstolpe 1951). There are four unpublished specimens of the Green-tailed Goldenthroat for the Madeira River drainage in central Amazonia deposited at MPEG in addition to our specimen. Two males (MPEG 35582–35583) and one female (MPEG 35584) were collected on 12 and 13 September 1982 by D. C. Oren and M. S. Brígida in shrubby *campina* at Campo das Flores, municipality of Borba (4° 24′ S, 59° 35′ W; coordinates obtained from Paynter and Traylor 1991), State of Amazonas. Another male (MPEG 19971) was collected between 13 and 26 July 1962 by José Hidasi at Guajará-Mirim (10° 48′ S, 65° 22′ W; coordinates from Paynter and Traylor 1991), State of Rondônia on the eastern bank of the Mamoré River on the border with Bolivia. The Green-tailed Goldenthroat has not been recorded for patches of *cerrado* in the neighboring Bolivian departments of Beni and Santa Cruz (Bates et al. 1992, Brace and Hornbuckle 1998, Pearce-Higgins 2000).

Horned Sungem—*Heliactin bilophus*. A male Horned Sungem was observed and tape-recorded on 8 November 2003 on the edge of gallery forest surrounded by natural wet grassland and open *cerrado* at FPF. The Horned Sungem is widely distributed in the *cerrados* of central Brazil and eastern Bolivia, but has a patchy distribution in Amazonia with all records from its southern (Brazilian states of Acre and Rondônia; Sick 1997) and northeastern (Surinam and Brazilian State of Amapá; Haverschmidt and Mees 1994, Silva et al.

1997) fringes. Our record is apparently the first for the Brazilian State of Amazonas.

Toco Toucan—*Ramphastos toco*. An adult female Toco Toucan was collected (MPEG 57564) on 14 November 2003 in an orchard at FPF. The Amazonian (nominate) population of the Toco Toucan occurs in patches of open and semi-open habitats along the Amazon River Valley between Manaus and the Marajó/Mexiana islands in Brazil (Henriques and Oren 1997, Sick 1997), and also in isolated enclaves of *cerrado* scattered throughout the Guyana shield in the Brazilian states of Amapá, Pará, and Roraima (Snethlage 1914, Pinto 1966, Novaes 1974) and neighboring countries of French Guyana, Suriname, and Guyana (Short and Horne 2002). The specimen collected in the BX-044 polygon has a pure white (instead of light yellow) throat with only a faint trace of red (instead of bold red) along the throat's lower border. This agrees with the diagnostic characters of subspecies *albogularis*, reported so far only for central South America (Short and Horne 2002). The overall size and bill length of MPEG 57564 are similar to those of specimens belonging to the nominate form, which is considerably bigger and heavier than *albogularis* (Todd 1943). Thus, MPEG 57564 clearly shows intermediate characters between the only two taxa recognized for the Toco Toucan (Short and Horne 2002). Further sampling of Toco Toucan populations along the Amazonia/*cerrado* ecotone in Brazil, Bolivia, and southeastern Peru may resolve the intricate geographic variation in this species (Todd 1943).

Collared Crescentchest—*Melanopareia torquata*. At least five Collared Crescentchest individuals were tape-recorded at FBV, FC, and FPF between 10 and 16 November 2003 in open and stony *cerrado* with tall grass. A single specimen was collected on 16 November after intensive tape-recording and play-back at FC (MPEG A8583; preserved in alcohol). This record is the first for the Brazilian State of Amazonas and the third for Amazonia after that of Pinto and Camargo (1957) for Serra do Cachimbo and Novaes (1960) for Gorotire, two other *cerrado* enclaves in the State of Pará, ~750 and 1,000 km, respectively, east of the BX-044 polygon (Fig. 1). The other nearest known records to the BX-044 polygon are from several localities in the State of Mato Grosso within the *cerrado*–Amazonia ecotone (Naumburg 1930, Silva and Oniki 1988, Silveira and D'Horta 2002) ~650 km to the south.

Ferruginous-backed Antbird—*Myrmeciza ferruginea*. A single adult male Ferruginous-backed Antbird was netted and collected on 31 October 2003 in sandy-soil *terra-firme* forest at KM 137 (MPEG 57660). No other individuals of this species were recorded during our fieldwork in the BX-044 polygon. The Ferruginous-backed Antbird was known from south of the Amazon River (where subspecies *eluta* occurs) prior to our record only for the lower portion of the Madeira-Tapajós interfluve (Zimmer and Isler 2003) with Flexal (~5° 97′ S, 56° 75′ W along the Transamazonian highway near Jacareacanga in southwestern Pará) being the southernmost locality where the species had been recorded (MPEG 47809, a female collected by G. P. Silva on 1 Dec 1973). Our record extends the known range of subspecies *eluta* ~600 km southwest including the southern-central part of the Madeira-Tapajós interfluve.

Pale-faced Bare-eye—*Skutchia borbae*. Four females and one male Pale-faced Bare-eye were netted and collected between 26 October and 1 November 2003 in sandy-soil *terra-firme* forest at KM 126 (MPEG 57691–57695, all adults). This range-restricted species is endemic to Brazil and the Madeira-Tapajós interfluve with its previously known southern record from the eastern bank of the lower Aripuanã River, State of Amazonas (Zimmer and Isler 2003). Our record extends the known range of the Pale-faced Bare-eye nearly 400 km southwest across the Aripuanã River, and into the south-central part of the Madeira-Tapajós interfluve.

Narrow-billed Woodcreeper—*Lepidocolaptes angustirostris*. We observed and tape-recorded two pairs of Narrow-billed Woodcreepers on 8 and 10 November 2003 in open *cerrado* near patches of gallery forest at FBV and FPF, respectively. Both pairs responded vigorously to play-back calls. All individuals observed exhibited the same field marks distinguishing the "*bivittatus*" group in this geographically variable polytypic species. Only two other apparently isolated populations of this *cerrado*-specialist woodcreeper (all belonging to the "*bivittatus*" group) are known for Amazonia: (1) Surinam, and (2) Brazilian states of Amapá and Pará, where it occurs on both banks of the lower Amazon River Valley between Santarém and Marajó Island (several MPEG specimens; Henriques and Oren 1997, Sanaiotti and Cintra 2001, Marantz et al. 2003). Our record appears to be the first for the Brazilian State of Amazonas indicating the Narrow-billed Woodcreeper has a much wider distribution in Amazonia than previously thought.

Pale-breasted Spinetail—*Synallaxis albescens.* Several individuals of Pale-breasted Spinetail were heard and seen between 8 and 17 November 2003 in open *cerrado* and grassland at FBV and FC; nearly all birds recorded were giving the species unmistakable, bisyllabic song. Our record is the second for an isolated population of the Pale-breasted Spinetail in a southern Brazilian Amazonia *cerrado* enclave after that reported by Pinto and Camargo (1957) for Serra do Cachimbo (Fig. 1) and confirmed since by additional specimens deposited at MPEG.

Pearly-vented Tody-tyrant—*Hemitriccus margaritaceiventer.* Several pairs of Pearly-vented Tody-tyrant were observed and tape-recorded between 12 and 16 November 2003 at FC and FCA in shrubby *cerrado* with a dense understory covered by epiphytic bamboo. Calling individuals were difficult to observe in the thick bamboo-dominated understory, but would fly to more open spaces after use of play-back calls. Our record represents the first for a *cerrado* enclave in southern Amazonia; populations in other Amazonian open and semi-open habitat enclaves occur in eastern Colombia and southern Venezuela (Fitzpatrick et al. 2004). The nearest record of Pearly-vented Tody-tyrant to the BX-044 polygon is from the *cerrado*–rainforest ecotone, >600 km to the south (Willis and Oniki 1990).

Common Tody-flycatcher—*Todirostrum cinereum.* A male Common Tody-flycatcher was collected (MPEG 57734) on 14 November 2003 in disturbed *cerrado* at FCA; during previous and subsequent days, other individuals were seen and heard in *cerrado* at this same locality and also at FBV and FPF. This record represents a major range extension for the Common Tody-flycatcher into central and western Amazonia, two regions where the species was considered to be absent (Ridgely and Tudor 1994, Fitzpatrick et al. 2004). The nearest records to the BX-044 polygon are from *cerrado* patches in the Cuiabá area, State of Mato Grosso, >900 km to the south (Naumburg 1930, Willis and Oniki 1990).

Plain-crested Elaenia—*Elaenia cristata.* Three adult males and one adult female Plain-crested Elaenia were collected on 13 and 14 November 2003 at FC and FPF (MPEG 57711–57714). Plain-crested Elaenias were among the most common birds at these localities occurring in *cerrado.* This open-habitat specialist species in Amazonia is distributed primarily in its eastern and northern portions with few scattered records for the central and western areas (Fitzpatrick et al. 2004). Isolated populations of the Plain-crested Elaenia in south-central and southwestern Amazonia, prior to our records, have been reported only for southeastern Peru, western Bolivia, and Serra do Cachimbo in the State of Pará (Pinto and Camargo 1957, Fitzpatrick et al. 2004). Unpublished specimens at MPEG indicate a much wider distribution in this sector of Amazonia than previously known in association with enclaves of *cerrado* and *campina*: MPEG 15420 collected by José Hidasi on 20 November 1955 at Itaituba (4° 17′ S, 55° 59′ W), west bank of the Tapajós River, southwestern Pará, and five additional specimens (MPEG 35482–35486), collected by D. C. Oren and M. S. Brígida between 12 and 20 September 1982 at Campo das Flores (4° 24′ S, 59° 35′ W), municipality of Borba, State of Amazonas, east bank of the lower Madeira River.

Lesser Elaenia—*Elaenia chiriquensis.* An adult female Lesser Elaenia (MPEG 57715) was netted and collected on 13 November 2003 in open *cerrado* at FC. The Lesser Elaenia in Amazonia occurs predominantly in open vegetation patches north of the Amazon and east of the Tapajós rivers with only about a handful of records for the south-central and southwestern parts of the basin, west of the Tapajós River (Marini and Cavalcanti 1990, Fitzpatrick et al. 2004). Our record indicates a more extensive distribution in south-central and southwestern Amazonia. This is reinforced by three previously unpublished specimens at the MPEG (49550–49552; two males and one unknown gender individual) collected by D. C. P. Neto on 15 October and 6 November 1991 in open *cerrado* near Humaitá on the left bank of the upper Madeira River (7° 31′ S, 63° 02′ W; Paynter and Traylor 1991) ~200 km west of the BX-044 polygon (Fig. 1).

Bearded Tachuri—*Polystictus pectoralis.* Two Bearded Tachuris were collected on 11 November 2003 in tall grassland with scattered low bushes at FPF. Both individuals were observed for a long time prior to collection while perched together on the same branch of a low bush ~30 cm above ground level. No additional individuals of Bearded Tachuri were recorded in the study area. A comparison of the specimens collected in the BX-044 polygon with series of the Bearded Tachuri at the MPEG, MNRJ (Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil), and MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil) revealed they are the subspecies *brevipennis* (significantly shorter-winged than the nominate form), which was previously known to occur only in the savannas of northern South America (Colombia, Venezuela, Guyana, Surinam, and Brazilian states of Roraima, Pará, and Amapá; Fitzpatrick et al. 2004; Fig. 1). Our records represents a major range extension for the Bearded Tachuri in Amazonia with the nearest previous records from >1,000 km to the south (where the nominate form is found locally in the *cerrados* of central Brazil and eastern Bolivia) and ~1,200 km to the north from the savannas of the Brazilian State of Roraima (where populations of *brevipennis* are quite numerous; Fitzpatrick et al. 2004; Fig. 1). Assigning the BX-044 polygon population to subspecies *brevipennis* suggests that Amazonian populations of Bearded Tachuri are apparently each other's closest relatives to the exclusion of the central South American population. This hypothesis should be further investigated by a detailed multi-character taxonomic study.

Rufous-sided Pygmy-tyrant—*Euscarthmus rufomarginatus.* A male Rufous-sided Pygmy-tyrant was tape-recorded and observed on 9 November 2003 while singing with its supposed mate and subsequently collected (MPEG 57705) in slightly disturbed shrubby *cerrado* at FBV. Two days later, another pair was tape-recorded in dense shrubby and tall grassy *cerrado* at FPF; no other individuals of this rare and patchily distributed flycatcher were located in the BX-044 polygon. Our records represents the most western and fourth published report of the Rufous-sided Pygmy-tyrant for an Amazonian *cerrado* enclave after those from Serra do Cachimbo in the State of Pará (Pinto and Camargo 1957) (Fig. 1), Sipaliwini in southern Surinam (Mees 1968), and a site 48 km north of Macapá, State of Amapá, Brazil (Silva et al. 1997). The nearest record of this species to the BX-044 polygon is from the *cerrado*–rainforest ecotone in the State of Mato Grosso (Serra das Araras) ~600 km to the south (Parker and Willis 1997).

Gray Monjita—*Xolmis cinereus.* A male collected on 13 November 2003 in a recently grazed crop field near an open *cerrado* patch at FBV (MPEG 57741) represents one of the few records of this species west of the Tapajós River into western Amazonia. It is apparently the first for the Brazilian State of Amazonas; other records for western Amazonia include those from *cerrado* enclaves in southeastern Peru and northern Bolivia (Graham et al. 1980). The nearest previous record of Gray Monjita to the BX-044 polygon is from the Guaporé River Valley in the *cerrado*–rainforest ecotone >700 km to the south (Silveira and D'Horta 2002).

White-rumped Monjita—*Xolmis velatus.* Two individuals observed briefly on 10 and 13 November 2003 in open *cerrado* near FBV and FPF, respectively, represent the first report of this species for south-central Amazonia and the Brazilian State of Amazonas. The nearest confirmed records of White-rumped Monjita to the BX-044 polygon are from the Guaporé River Valley (State of Mato Grosso) in the *cerrado*–rainforest ecotone >700 km to the south (Silveira and D'Horta 2002).

Masked Gnatcatcher—*Polioptila dumicola.* Two adult male Masked Gnatcatchers were tape-recorded and collected on 10 and 14 November 2003, respectively, in grassland with scattered low bushes at FPF (MPEG 57773) and in disturbed *cerrado* at FCA (MPEG 57772). This species was also regularly recorded between 9 and 17 November in gallery forest and denser *cerrado* at FBV. This represents the first record of this species for a *cerrado* enclave in Amazonia; the nearest previous record of Masked Gnatcatcher to the BX-044 polygon is from the *cerrado*–rainforest ecotone in the State of Mato Grosso

>700 km to the south (Silveira and D'Horta 2002).

Pale-breasted Thrush—*Turdus leucomelas.* An adult male Pale-breasted Thrush was netted and subsequently collected on 12 November 2003 in gallery forest at FBV. A second individual was continuously observed and eventually tape-recorded between 10 and 17 November 2003 at FPF. This represents one of the few records of this species for south-central Amazonia, besides those from other *cerrado* enclaves at Serra do Cachimbo, southern Pará (Pinto and Camargo 1957) and Humaitá, southern Amazonas (~200 km west of the BX-044 polygon, across the Madeira River) where two previously unpublished specimens (MPEG 49573–49574) were collected by D. C. P. Neto on 20 and 30 October 1991.

Chalk-browed Mockingbird—*Mimus saturninus.* An adult female Chalk-browed Mockingbird was collected on 10 November 2003 in open grassland with scattered low bushes at FPF; several pairs and small groups of this species were regularly observed between 8 and 17 November 2003 in open *cerrado* in the BX-044 polygon. This represents the first record of this species for a *cerrado* enclave in southern Amazonia. The nearest record of Chalk-browed Mockingbird to the BX-044 polygon is from the *cerrado*–rainforest ecotone in the State of Mato Grosso >700 km to the south (Silveira and D'Horta 2002).

Yellowish Pipit—*Anthus lutescens.* Several individual Yellowish Pipits were regularly seen and heard between 9 and 17 November 2003 in grassland and recently grazed crop fields at FBV and FPF. This record is the first for a *cerrado* enclave in southern Brazilian Amazonia. The nearest previous records of Yellowish Pipit to the BX-044 polygon is from the *cerrado*–rainforest ecotone in the State of Mato Grosso >700 km to the south (Silveira and D'Horta 2002).

White-lined Tanager—*Tachyphonus rufus.* An adult male White-lined Tanager was tape-recorded and collected (MPEG 57786) on 10 November 2003 in disturbed gallery forest at FPF; no other individuals were recorded during our survey in the BX-044 polygon. This record is a major range extension; the nearest published records to the BX-044 polygon are from Tapirapuã, Mato Grosso on the *cerrado*–rainforest ecotone (~800 km to the southeast; Naumburg 1930) and Mirituba, Pará (~850 km to the northeast; Griscom and Greenway 1941).

Spotted Tanager—*Tangara punctata.* A lone Spotted Tanager was observed on 25 October 2005 for several minutes while foraging in the canopy of a small tree on the edge of sandy-soil *terra-firme* forest at KM 126. This represents the southwestern most record of this species whose distribution stronghold is in the Guyana shield and southeastern Amazonia (Ridgely and Tudor 1989, Isler and Isler 1999). The nearest records to the BX-044 polygon include those from Alta Floresta, State of Mato Grosso (~650 km to the southeast; Zimmer et al. 1997), and Serra do Cachimbo, State of Pará (~750 km to the east; Pinto and Camargo 1957).

Rufous-collared Sparrow—*Zonotrichia capensis.* An adult male Rufous-collared Sparrow was tape-recorded and collected (MPEG 57803) on 10 November 2003 in an open disturbed field at FPF; several other individuals of this species were regularly recorded in open habitats in the BX-044 polygon during our survey. This record is the third for a southern Amazonian *cerrado* enclave after those from Serra do Cachimbo and the upper Cururu River area, both in the State of Pará (Pinto and Camargo 1957; also specimens MPEG 22408–22409, 22412). The nearest records to the BX-044 polygon are those from the upper Cururu River (>400 km to the northeast) and the *cerrado*–rainforest ecotone in the State of Mato Grosso >700 km to the south (Silveira and D'Horta 2002).

Wedge-tailed Grass-finch—*Emberizoides herbicola.* Two Wedge-tailed Grass-finch specimens were collected at FPF (MPEG 57803–57804) on 10 and 11 November 2003, respectively. Wedge-tailed Grass-finches were seen or heard on a daily basis in open habitats during our survey in the BX-044 polygon. This new record of Wedge-tailed Grass-finch is the first for a *cerrado* enclave in southern Brazilian Amazonia. Three other previously unpublished specimens at MPEG (49609–49611) document the species' presence at Campos de Humaitá in the State of Amazonas ~200 km west of the BX-044 polygon across the Madeira River (Fig. 1). The nearest previously published reports of Wedge-tailed Grass-finch to the BX-044 polygon are from the *cerrado*–rainforest ecotone in the State of Mato Grosso >700 km to the south (Silveira and D'Horta 2002).

Plumbeous Seedeater—*Sporophila plumbea.* Two males, a female, and an unknown gender specimen of Plumbeous Seedeater were collected between 9 and 11 November 2003 in open grassland with scattered low bushes at FBV and FPF (MPEG 57808–57811); MPEG 57810 had its territorial song tape-recorded prior to collection. The Plumbeous Seedeater was common in open grassland in the BX-044 polygon. Previous records of this species for southern Amazonian *cerrado* enclaves are from Pampas del Heath, Peru (Graham et al. 1980), two localities in the Department of Beni, Bolivia (Gyldenstolpe 1945), and Serra do Cachimbo, State of Pará (Pinto and Camargo 1957). The nearest records of Plumbeous Seedeater to the BX-044 polygon are from Serra do Cachimbo and the *cerrado*–rainforest ecotone in the State of Mato Grosso, both >750 km to the east and south, respectively (Pinto and Camargo 1957, Silveira and D'Horta 2002).

Capped Seedeater—*Sporophila bouvreuil.* An adult male Capped Seedeater was observed for several minutes with five females or immature individuals on 16 November 2003 while perching on planted grasses growing by a ranch garden at FPF along the "Estanho" road. Prior to our record, the Capped Seedeater had been reported in Amazonia only for its eastern edge (Marajó Island and the State of Pará), and the Sipaliwini *cerrado* enclave in Surinam (Ridgely and Tudor 1989), all >1,000 km from the BX-044 polygon.

CONSERVATION IMPLICATIONS

Cerrado patches can contribute significantly to local avian species richness in southern Amazonia in addition to supporting species with special relevance for conservation whose ranges are centered in the *cerrado* biome of central and northern South America (e.g., Bearded Tachuri and Rufous-sided Pygmy-tyrant; IUCN 2006). Amazonian *cerrado* enclaves such as the BX-044 polygon constitute unique conservation areas as they: (1) usually encompass the wide range of vegetation types covering the complex mosaic of soils associated with the transition between forested and non-forested habitats allowing the conservation of areas with high inter-habitat diversity, and (2) are inhabited by disjunct populations of typical *cerrado* species whose ranges have been adversely affected by widespread conversion of native habitats to crop fields in central Brazil (Klink and Machado 2005). Conservation of *cerrado* enclaves offer the rare opportunity to combine preservation of sharp ecotonal zones with high inter-habitat diversity in Amazonia with establishment of a complementary network of conservation units directed at preserving the *cerrado* biome throughout South America.

Rice fields and logging concessions are continuing to move farther into the BX-044 polygon. Thus, neighboring and only partially overlapping indigenous reservations are becoming the only areas in the polygon with no or low human impact. The sole alternative to widespread and imminent de-characterization of the unique natural landscape and biodiversity of the BX-044 polygon is the urgent establishment of a new conservation unit encompassing all or most of the polygon.

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APPENDIX. Birds recorded at the BX-044 polygon, Brazilian Amazonia, between 24 October and 17 November 2003. Nomenclature follows the Brazilian Check-list Committee (CBRO 2006). Key: D^1 = Documentation obtained for a given species. T = tape recorded. C = collected (specimens deposited at the Museu Paraense Emílio Goeldi – MPEG - in Belém, Pará, Brazil). Species without any documentation code were only seen or heard. Habitats^2: TF = *terra-firme* forest, RF = riparian forest, GF = gallery forest, CP = *campinarana*, C = *cerrado*, G = grassland, M = man-made, disturbed habitats. Numbers within habitats refer to the following localities where the species was recorded: 1 = "KM 137", 2 = "KM 126", 3 = FPF "Fazenda Passo Formoso", 4 = FCA "Fazenda Campo Alegre", 5 = FBV "Fazenda Bela Vista", and 6 = FC "Fazenda Copeares". sp.^{3} = undescribed taxon; description in preparation.

Family (*n* species) Species	D^1	Habitats^2						
		TF	RF	GF	CP	C	G	M
Tinamidae (9)								
Tinamus major	T		2					
T. guttatus	T	1	2		2			
Crypturellus cinereus	T	1	2	3	2			
C. soui	T	1		3	2			
C. undulatus	T			3, 5				
C. strigulosus		1						
C. variegatus		1	2		2			
C. parvirostris						3, 5	3, 5	
Rhynchotus rufescens						5, 6	5	
Anatidae (1)								
Dendrocygna viduata							3, 5	2
Cracidae (4)								
Ortalis guttata						3		
Penelope jacquacu	C	1	2		2			
Aburria cujubi			2					
Mitu tuberosum		1	2					
Odontophoridae (1)								
Odontophorus gujanensis			2		2			
Ardeidae (5)								
Butorides striatus								1
Bubulcus ibis								2
Ardea alba							3, 5	2
Pilherodius pileatus							5	
Egretta thula							3, 5	2
Cathartidae (4)								
Cathartes aura						3, 4, 5, 6	3, 5	
C. melambrotus		1	2		2			
Coragyps atratus								2
Sarcoramphus papa						6		

APPENDIX. Continued.

Family (*n* species) Species	D[1]	Habitats[2]						
		TF	RF	GF	CP	C	G	M
Accipitridae (8)								
Elanoides forficatus		1	2		2			
Gampsonyx swainsonii	C				2			3
Elanus leucurus						5		
Ictinia plumbea		1	2		2		3	
Heterospizias meridionalis						3	3	
Rupornis magnirostris						3, 4, 5	3	
Buteo albicaudatus						3, 5	5	
Spizaetus ornatus	T	1						
Falconidae (8)								
Daptrius ater	T	1	2					
Ibycter americanus	T	1	2					
Caracara plancus							5	
Milvago chimachima						3, 5	3, 5	
Herpetotheres cachinnans						3	3	
Micrastur ruficollis		1						
M. semitorquatus	T		2		2			
Falco rufigularis	C				2, 3	3		
Psophiidae (1)								
Psophia viridis		1	2					
Rallidae (2)								
Laterallus viridis	T					3, 5	3, 5	2
Porzana albicollis							3, 5	
Charadriidae (1)								
Vanellus chilensis							3, 5	2
Scolopacidae (4)								
Gallinago paraguaiae	T, C						3, 5	
Tringa melanoleuca							3, 5	
T. flavipes	C						3, 5	
T. solitaria	C						3, 5	
Columbidae (7)								
Columbina passerina						3, 4, 5	3, 5	
C. talpacoti							3, 5	
Uropelia campestris	C						3	
Patagioenas speciosa				3	2	3, 4	3, 5	
P. cayennensis				3	2	3, 4		
Leptotila rufaxilla		1	2					
Geotrygon montana		1	2		2			
Psittacidae (13)								
Ara ararauna					2	5		
A. chloropterus		1						
Orthopsittaca manilata	T, C			3, 6	2	3, 4, 5, 6	3, 5	
Diopsittaca nobilis						6		
Aratinga leucophthalma	T				2	3, 4, 5, 6		
A. aurea	C					4, 5, 6		
Pyrrhura snethlageae	T, C	1						
Forpus xanthopterygius								3
Brotogeris chiriri	T		2	6	2	3, 6		
Touit huetii	T					5		
Pionus menstruus		1	2	2, 3	2			
Amazona kawalli	T	1	2					
A. amazonica	T			3				

APPENDIX. Continued.

Family (*n* species) Species	D^1	Habitats^2						
		TF	RF	GF	CP	C	G	M
Cuculidae (4)								
Piaya cayana		1	2		2			
P. melanogaster	T	1						
Crotophaga ani							3, 5	
Tapera naevia	T					3, 4, 5	5	
Strigidae (3)								
Megascops choliba					2	3, 5		
Glaucidium hardyi			2					
Athene cunicularia							3	
Nyctibiidae (1)								
Nyctibius griseus			2			3		
Caprimulgidae (5)								
Lurocalis semitorquatus		1						
Chordeiles pusillus	C					4		
Chordeiles sp.								2
Caprimulgus maculicaudus	C						5	
Hydropsalis torquata	C					3, 4, 5, 6	3, 5	
Apodidae (3)								
Chaetura cinereiventris	T	1						
C. meridionalis						3, 5	3, 5	
Tachornis squamata				3		3	3, 5	
Trochilidae (13)								
Phaethornis nattereri	C			5				
P. ruber	C	1	2		2			
P. pretrei							5	3
P. philippii	C	1	2		2			
P. malaris	C		2					
Campylopterus largipennis	C	1	2		2			
Eupetomena macroura	C					5, 6		
Anthracothorax nigricollis	T					3	3	
Thalurania furcata	T, C	1		6	2			
Polytmus theresiae	C					6		
Heliothryx auritus		1						
Heliactin bilophus	T					5	3	
Heliomaster longirostris					2			
Trogonidae (5)								
Trogon viridis	T	1	2		2			
T. curucui	T			3, 6	2			
T. violaceus	T	1	2		2			
T. melanurus	T	1	2		2			
Pharomachrus pavoninus	T	1						
Alcedinidae (1)								
Chloroceryle aenea	C		2					
Momotidae (3)								
Electron platyrhynchum	C	1	2					
Baryphthengus martii	C	1						
Momotus momota	T		3		2	3		
Galbulidae (4)								
Galbula cyanicollis	C	1	2					

APPENDIX. Continued.

Family (*n* species) Species	D[1]	Habitats[2]						
		TF	RF	GF	CP	C	G	M
G. ruficauda	C			3		3		2
G. leucogastra	T, C				2			
G. dea	T	1						
Bucconidae (5)								
Notharchus hyperrhynchus	T	1			2			
Nystalus chacuru	C					3	3, 5	
Malacoptila rufa	C	1						
Monasa morphoeus	C	1	2		2			
Chelidoptera tenebrosa		1			2	3, 5, 6		
Ramphastidae (7)								
Ramphastos toco	C					3	3	
R. tucanus	T	1		3	2			
R. vitellinus	T	1	2	3	2			
Selenidera gouldii		1						
Pteroglossus bitorquatus	C	1						
P. castanotis					2	3		2
P. beauharnaesii	T	1						
Picidae (9)								
Picumnus aurifrons	T	1						
Melanerpes cruentatus	C	1	2	3, 6	2	5		3
Veniliornis passerinus						5		
V. affinis		1	2		2			
Piculus flavigula		1	2					
P. chrysochloros	T	1						
Celeus grammicus	C	1						
Campephilus rubricollis	T	1	2		2			
C. melanoleucos			2					
Melanopareiidae (1)								
Melanopareia torquata	T, C					3, 5, 6	3, 5	
Thamnophilidae (36)								
Cymbilaimus lineatus		1	2		2			
Thamnophilus doliatus	T					5, 6		2
T. aethiops	T	1						
T. schistaceus	T, C	1						
T. stictocephalus	T, C			6	2	6		
T. amazonicus	T		2					
Thamnomanes saturninus	C	1						
T. caesius	T, C	1	2		2			
Megastictus margaritatus	C	1			2			
Pygiptila stellaris	C	1	2		2			
Myrmotherula haematonota	T, C	1	2		2			
M. brachyura		1	2		2			
M. sclateri	T	1	2					
M. hauxwelli	T, C	1	2		2			
M. axillaris	T, C	1	2		2			
M. longipennis	C	1	2					
M. menetriesii		1	2		2			
Herpsilochmus sp.[3]	T, C	1	2		2			
Formicivora grisea	C					6		
F. rufa	T, C					5, 6	5	
Terenura humeralis	T	1						
Cercomacra cinerascens		1	2		2			

APPENDIX. Continued.

Family (*n* species) Species	D[1]	Habitats[2]						
		TF	RF	GF	CP	C	G	M
C. nigrescens	T, C	1		6	2			
Myrmoborus myotherinus	T, C	1	2		2			
Hypocnemis cantator	T, C	1	2		2			
Sclateria naevia			2					
Schistocichla leucostigma	T, C	1	2		2			
Myrmeciza ferruginea	C	1						
M. hemimelaena	T	1	2		2			
M. atrothorax	T, C	1		3, 5	2			
Rhegmatorhina hoffmannsi	C	1						
Hylophylax naevius	T, C	1	2		2			
H. punctulatus	T, C				2			
H. poecilinotus	C	1	2		2			
Phlegopsis nigromaculata	C	1	2		2			
Skutchia borbae	C	1						
Conopophagidae (1)								
Conopophaga melanogaster	C				2			
Grallariidae (1)								
Myrmothera campanisona	T	1						
Rhinocryptidae (1)								
Liosceles thoracicus	T	1						
Formicariidae (1)								
Formicarius colma	C	1	2		2			
Scleruridae (2)								
Sclerurus rufigularis	T, C	1			2			
S. caudacutus	T, C	1	2		2			
Dendrocolaptidae (15)								
Dendrocincla fuliginosa		1						
D. merula	C	1	2		3			
Deconychura longicauda		1						
D. stictolaema	C	1	2					
Sittasomus griseicapillus	T, C	1	2		2			
Glyphorynchus spirurus	C	1	2		2			
Hylexetastes uniformis	C				2			
Dendrocolaptes certhia	T				2			
D. hoffmannsi	C	1						
Xiphorhynchus picus	T	1		6				2
X. elegans	T, C	1	2		2			
X. guttatus	T	1						
Lepidocolaptes angustirostris	T			3, 5		3, 5	3, 5	
L. albolineatus		1						
Campylorhamphus procurvoides	T, C	1	2					
Furnariidae (11)								
Synallaxis albescens					2	5		
S. hypospodia	T						5	
S. rutilans	C	1						
Berlepschia rikeri				3, 5				
Hyloctistes subulatus	T, C	1	2					
Philydor erythrocercum		1	2					
P. erythropterum	T, C	1	2					
P. pyrrhodes	C	1						
Automolus ochrolaemus	C	1	2					

APPENDIX. Continued.

Family (*n* species) Species	D[1]	Habitats[2]						
		TF	RF	GF	CP	C	G	M
A. paraensis	C	1						
Xenops minutus	C	1	2		2			
Tyrannidae (50)								
Mionectes oleagineus	T, C	1	2		2			
Leptopogon amaurocephalus	T				2			
Corythopis torquatus	T				2			
Hemitriccus minor	T, C	1	2		2			
H. striaticollis	T					3		
H. margaritaceiventer	T					4, 6		
H. minimus	T	1			2			
Poecilotriccus latirostris	T					5	5	
Todirostrum cinereum	C					3, 4, 5		
Tyrannulus elatus	T	1						2
Myiopagis gaimardii	T	1	2	3				
Elaenia flavogaster	T, C					3, 5		
E. cristata	C					3, 5, 6		
E. chiriquensis	T, C					3, 5, 6		
Ornithion inerme	T	1	2					
Suiriri islerorum	T, C					3		
Polystictus pectoralis	T, C						3	
Euscarthmus rufomarginatus	T, C						5	
Zimmerius gracilipes	T	1						
Sublegatus modestus	T, C					3		
Myiornis ecaudatus		1	2		2			
Rhynchocyclus olivaceus	T, C	1						
Tolmomyias assimilis	T, C	1						
T. flaviventris	T					3, 6		3
Platyrinchus saturatus	T, C	1						
P. coronatus	C		2					
P. platyrhynchos		1						
Onychorhynchus coronatus	C		2		2			
Myiophobus fasciatus							5	
Myiobius barbatus	C	1	2					
M. atricaudus	C	1	2					
Terenotriccus erythrurus	T, C	1	2		2			
Lathrotriccus euleri	T, C			3	2			
Xolmis cinereus	T, C						5	
X. velatus						3		
Colonia colonus						5	5	
Legatus leucophaius					2			3
Myiozetetes cayanensis								2, 3
Pitangus sulphuratus						3,4, 5, 6	3, 5	2, 3
Conopias parvus	T, C	1			2			
Megarynchus pitangua	C				2	3	3	3
Tyrannopsis sulphurea	T, C			6				
Tyrannus albogularis	T, C						3, 5	
T. melancholicus	C					3, 4, 5, 6	3, 5	2
T. savanna								3
Rhytipterna simplex	T	1	2		2			
Myiarchus tuberculifer	T	1	2					
M. swainsoni	T					5		
M. ferox	C					3, 4, 5	3, 5	
Ramphotrigon ruficauda	T, C	1						
Cotingidae (5)								
Phoenicircus nigricollis	T, C	1						

APPENDIX. Continued.

Family (*n* species) Species	D[1]	Habitats[2]						
		TF	RF	GF	CP	C	G	M
Cotinga cayana		1						
Lipaugus vociferans	T, C	1						
Xipholena punicea	T	1						
Querula purpurata		1						
Pipridae (8)								
Tyranneutes stolzmanni	T	1	2		2			
Piprites chloris		1						
Lepidothrix nattereri	C	1	2		2			
Manacus manacus	C			3				
Chiroxiphia pareola	T, C	1	2		2			
Xenopipo atronitens	T, C				2			
Heterocercus linteatus	T, C		2					
Pipra rubrocapilla	T, C	1	2		2			
Tityridae (6)								
Schiffornis turdina	C	1	2		2			
Laniocera hypopyrra	C	1						
Tityra cayana		1						3
T. semifasciata		1						
Pachyramphus marginatus		1						
P. minor	T	1						
Vireonidae (5)								
Vireolanius leucotis	T	1	2		2			
Vireo olivaceus	T			3				
Hylophilus pectoralis	T			6				
H. hypoxanthus	T	1	2		2			
H. ochraceiceps	T	1						
Corvidae (1)								
Cyanocorax chrysops								2
Hirundinidae (4)								
Progne chalybea	C					3, 4, 5, 6	3, 5	2
Atticora fasciata							3, 5	2
Neochelidon tibialis	C							1
Stelgidopteryx ruficollis						3, 4, 5, 6	3, 4	2
Troglodytidae (5)								
Microcerculus marginatus	T, C	1						
Troglodytes musculus							3, 5	2
Thryothorus genibarbis	T, C			5, 6	2			
T. leucotis						5		
Cyphorhinus arada	C	1						
Polioptilidae (2)								
Ramphocaenus melanurus	T, C		2		2			
Polioptila dumicola	T, C			5, 6		4, 5		
Turdidae (4)								
Catharus fuscescens	C	1						
Turdus leucomelas	C					3		
T. lawrencii	T, C		2					
T. albicollis	T, C	1	2		2			
Mimidae (1)								
Mimus saturninus	C					3	3	

APPENDIX. Continued.

Family (*n* species) Species	D[1]	Habitats[2]						
		TF	RF	GF	CP	C	G	M
Motacillidae (1)								
Anthus lutescens							3	
Coerebidae (1)								
Coereba flaveola	T					3, 4, 5	3, 5	2
Thraupidae (20)								
Schistochlamys melanopis	C					3, 4, 5		2
Cissopis leverianus			2					
Lamprospiza melanoleuca	T	1	2		2			
Habia rubica	T		2					
Tachyphonus cristatus		1	2		2			
T. surinamus	T, C	1			2			
T. rufus	T, C							3
Lanio versicolor	T, C	1	2					
Ramphocelus carbo	C			5				2, 3
Thraupis episcopus								2, 3
T. palmarum	C							2
Tangara chilensis	C	1	2		2			
T. punctata		1						
T. gyrola	C	1						
T. cayana	C					3, 5	3, 5	
T. cyanicollis					2			
Tersina viridis							5	2
Dacnis lineata		1	2		2			
D. cayana					2	5		
Hemithraupis flavicollis		1	2		2	5		
Emberizidae (9)								
Zonotrichia capensis	T, C						3	
Ammodramus humeralis	C						3, 5	
Emberizoides herbicola	T, C						3, 5	
Volatinia jacarina	C						5	
Sporophila plumbea	T, C						3, 5	
S. lineola	C					3	3	
S. bouvreuil								3
S. angolensis	T, C			5		5	3, 5	
Arremon taciturnus	C					6		
Cardinalidae (2)								
Saltator maximus	T	1				3, 5		
Cyanocompsa cyanoides		1						
Parulidae (1)								
Phaeothlypis fulvicauda			2		2			
Icteridae (3)								
Psarocolius bifasciatus		1						
Cacicus cela	T, C	1	2		2	3, 4, 5, 6		2
Molothrus oryzivorus								2
Fringillidae (2)								
Euphonia chlorotica	T					5		3
E. rufiventris	T	1	2		2			

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MULTISCALE ANALYSIS OF TYRANNID ABUNDANCES AND LANDSCAPE VARIABLES IN THE CENTRAL PLAINS, USA

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ABSTRACT.—Effects of scale on relationships between organisms and their environment are of considerable contemporary interest. We evaluated Breeding Bird Survey data and landscape measures derived from aerial photographs to examine how relationships changed over a continuous range of 16 spatial scales. Analyses incorporated 1985–1994 data (average number of birds/stop/yr) for eight flycatcher species (Tyrannidae) for each of 50 stops on 198 Breeding Bird Survey transects in the Central Plains. Associations of bird abundances with landscape variables changed gradually with small changes in scale. Edge density had significant associations with abundances of Eastern Phoebes (*Sayornis phoebe*), Great Crested Flycatchers (*Myiarchus crinitus*), and Western Kingbirds (*Tyrannus verticalis*) suggesting this landscape characteristic is important for certain breeding flycatcher species. Fractal dimension and principal component II, the latter reflecting amounts of closed forest versus open country, exhibited the highest correlations with abundances of the greatest number of species. Correlations of abundances and landscape variables were highest at larger spatial scales, 17- to 50-stop segments (i.e., 13.7 and 40.2 km in length, respectively). Evaluating more than 2–3 spatial scales can provide insight into relationships of abundance of a species with potentially influential environmental factors. These analyses allow the data to indicate the most appropriate scale or scales for a particular study, rather than depending entirely on a researcher's subjective perception of what scales are important to a given species. *Received 21 February 2006. Accepted 9 October 2006.*

Habitat analyses show that different factors affect avian populations and diversity at different spatial scales (Böhning-Gaese 1997, Pribil and Picman 1997, MacFaden and Capen 2002). Vegetation structure is most important at a local (within-plot) level (Wiens et al. 1987, Pribil and Picman 1997), whereas measures such as community structure and amount of edge are most influential on bird communities at the landscape level (McGarigal and McComb 1995, Hagan et al. 1997). Perceived interactions among bird species can vary depending on the scale at which the study was conducted. For example, Sherry and Holmes (1988) found that Least Flycatchers (*Empidonax minimus*) negatively influenced the distribution of American Redstart (*Setophaga ruticilla*) territories at a small scale, but on a regional level the two species were positively associated.

Using a multiscale approach allows one to evaluate the effect of scale-dependent patterns on avian species (Wiens et al. 1987, Wiens 1989a, Kotliar and Wiens 1990). Several studies have examined the influence of habitat on avian populations at various scales (McGarigal and McComb 1995, Böhning-Gaese 1997, Pribil and Picman 1997, Drolet et al. 1999, Saab 1999, MacFaden and Capen 2002, Tarvin and Garvin 2002, Westphal et al. 2003, Brennan and Schnell 2005). However, relatively little work has been done comparing effects at more than three scale levels (Wiens et al. 1986, Meyer et al. 2002, Brennan and Schnell 2005). Wiens (1989b) and Wiens et al. (1987) recognized four levels of scale: (1) the biogeographic level involving an area sufficiently large to encompass different climates, vegetation formations, and assemblages of species; (2) the regional level encompassing many habitat patches and numerous local populations; (3) a local-patch level with a given patch being occupied by many individuals of several species; and (4) the within-plot level involving the space occupied by a single individual over some relevant time period. Different environmental factors may influence birds at particular scales and it is important to consider the appropriate scale for the question being asked (Wiens 1989b). However, it often is not readily apparent how one objectively selects the appropriate scale within one of these scale levels.

We evaluated bird abundances at local and somewhat less than regional scales as defined by Wiens (1989b) using data from Breeding

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Bird Survey transects in six states in the USA. The study region initially was selected to encompass the breeding range in the USA of the Scissor-tailed Flycatcher (*Tyrannus forficatus*); one finds the edges of breeding ranges of numerous other bird species in this region, which is characterized by considerable environmental variation and gradients. We analyzed a continuum of 16 scales from a local 0.8-km level (one stop on a transect and the adjacent strips of land) to a subregional 40.2-km level (all 50 stops). We were interested in: (1) examining how relationships between bird abundances and landscape variables change over various scale levels; (2) finding the scale or scales at which selected landscape variables have the strongest relationship to bird abundance; and (3) discovering which landscape variables have the strongest association with bird abundance. An important objective of our study was to investigate how data can be used to suggest more precisely the specific level at which local and subregional scales should be set, rather than depending solely on a researcher's perception of what is an appropriate scale. We selected eight species of breeding flycatchers (Tyrannidae) for this study that occur in the region and characterized the habitats occupied by these birds at various scales. Our intuitive prediction based on general knowledge of the species was that we would find the strongest associations of landscape features and bird abundances at the intermediate scales examined.

METHODS

Bird Data.—We used bird data collected on Breeding Bird Surveys, which are annual counts that provide information on relative abundances of bird species (Robbins et al. 1986). The surveys are conducted on more than 3,000 roadside transects on secondary roads throughout the United States and southern Canada. Each transect is 39.4 km (24.5 mi) in length and is surveyed once each year in June. An observer follows the designated route and conducts 50, 3-min point counts at 0.8-km (0.5-mi) intervals along the transect. All birds seen and heard during counts are recorded.

Our analyses incorporated Breeding Bird Survey data collected from 1985 to 1994 on 198 transects throughout Kansas, Oklahoma, Texas, Missouri, Arkansas, and Louisiana (Fig. 1) for eight species of flycatchers: Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virescens*), Eastern Phoebe (*Sayornis phoebe*), Vermillion Flycatcher (*Pyrocephalus rubinus*), Great Crested Flycatcher (*Myiarchus crinitus*), Western Kingbird (*Tyrannus verticalis*), Eastern Kingbird (*T. tyrannus*), and Scissor-tailed Flycatcher. These species are readily identified visually and/or by call, and most are not secretive. Thus, there was a relatively high probability of recording them if present—at least for some of the years covered by the study. These eight related species were all represented on a substantial number of routes within the overall study region. In addition, the species are known to have a range of habitat preferences.

The 198 transects used in our analyses were those that had been surveyed a minimum of five times in the 10-year period. The average number of birds per stop per year for each transect provided an average abundance index for each species at each of the 50 stops for each of the 198 transects.

We used a kriging method (van Horssen et al. 1999) for five species that occurred on less than 80% of the 198 transects to identify which transects were appropriately considered to be within the species' range and, therefore, should be included in the analysis. Kriging interpolates data values measured at irregularly spaced sample points to provide estimated values throughout an area. The five species analyzed only for a subset of the 198 possible transects were: Eastern Wood-Pewee (150 transects; Fig. 1A), Acadian Flycatcher (91; Fig. 1B), Eastern Phoebe (157; Fig. 1C), Vermilion Flycatcher (36; Fig. 1D), and Western Kingbird (124; Fig. 1F). The purpose of using kriging to delineate the extent of the range was to ensure that we were not including in analyses transects and their associated landscape cover values that were substantially outside the range for a given species. Although definition of the edge of a species' range is to some extent subjective, operationally the technique we used produced useful results given the purposes of our study.

Landscape Data.—Digital aerial photographs of the landscape along and adjacent to each of the 198 Breeding Bird Survey transects were obtained from the National Aerial Photography Program, U.S. Department of Agriculture. The photographs (scale 1:40,000)

TABLE 1. Number of adjacent stops evaluated for landscape characteristics along Breeding Bird Survey routes amalgamated for particular scale, segment length, and area. Segment length includes sum of distances between all adjacent stops within the segment plus one-half of the interval distance between end stops of the segment and adjacent stops that were not part of the segment.

No. stops segment	Length of segment		Area evaluated (ha)
	Miles	Kilometers	
1	0.5	0.8	1.93
2	1.0	1.6	3.86
3	1.5	2.4	5.79
4	2.0	3.2	7.72
5	2.5	4.0	9.66
6	3.0	4.8	11.59
7	3.5	5.6	13.52
8	4.0	6.4	15.45
9	4.5	7.2	17.38
10	5.0	8.0	19.31
11	5.5	8.9	21.24
12	6.0	9.7	23.17
17	8.5	13.7	32.83
22	11.0	17.7	42.49
25	12.5	20.1	48.28
50	25.0	40.2	96.56

were taken from December through March 1989, 1990, or 1991, depending on flight schedule, and captured the landscape structure present at about the midpoint of the years for which bird censuses were evaluated. There were land-cover changes during the decade for which bird data were analyzed and use of land-cover information from about the midpoint of that period provided reasonable estimates of the landscape features encountered by birds throughout the 10-year period.

The 198 transects covered an area that encompasses substantial changes in habitat, as well as marked differences in bird faunas. We used a belt transect to evaluate cover types for land adjacent to each bird transect (i.e., all land within ~1.2 km on either side and extending 0.4 km [0.25 mi] beyond each end of the transect). Thus, the total area analyzed for each transect was 40.2 km in length and approximately 2.4 km in width. The width of the belt transect was chosen in part because of practical considerations (e.g., the size of aerial photographs) and because it encompassed well the outer detection distance for the most readily observed tyrannids in the study. Previous studies by Certain (2000) and Brenner and Schnell (2005) categorized landscapes along these 198 transects into six cover types, which we also have used: urban, closed forest (<1 canopy width between trees), open forest (≥1 and <20 canopy widths between trees), open country (≥20 canopy widths between trees), water, and bare ground. This landscape classification system proved workable given the resolution possible from the aerial photographs. The scale of landscape analysis was such that it provided considerable inter- and intra-transect variation in landscape characteristics, but did not subdivide the landscape so finely to include large numbers of cover types that would be found in only a small subset of transects.

We digitized each transect into ArcInfo 8.x (Environmental Systems Research Institute, Inc., Redlands, CA, USA). Once digitized, transects were geo-rectified to provide accurate perimeter and area measurements. The transects were imported into ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to create a point-stop layer to mark locations where bird counts were made.

We evaluated 16 scales for each original transect to investigate scale influence on bird perception of their surrounding environment. A local scale of 0.80 km (segment length 1 = one point count and one-half of distance to each of two adjacent stops) was the smallest used. We increased segments by single stops until segment length equaled 12. We also evaluated segment lengths of 17, 22, 25, and 50 stops (Table 1). Our analyses involve evaluating landscape features at different scales using a fixed-width transect, a sampling procedure that has been used in a variety of ecological studies (e.g., Connell et al. 1997). The belt transect for landscape features essentially parallels the sampling frame used when conducting the bird surveys. Thus, we obtained quantified characterizations of the landscapes encountered by the birds at multiple scales.

Landscape metrics calculated based on formulations in FRAGSTATS (McGarigal and Marks 1995) for each segment length on each transect were: area-weighted mean patch fractal dimension, edge density, and patch density. This program considers that edges of the belt transect typically are not true habitat edges. These measures were chosen from an extensive list of possible metrics that can be com-

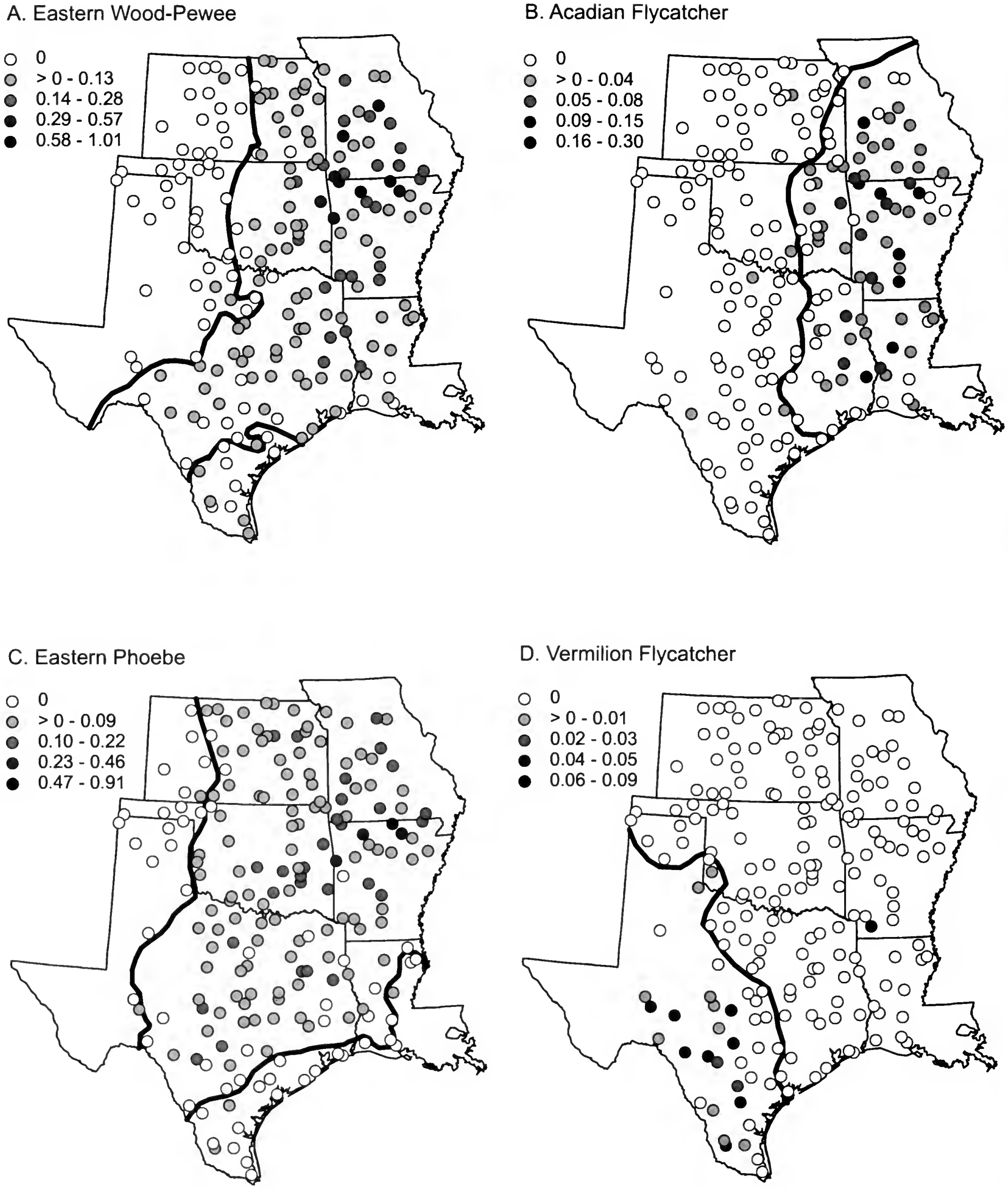

FIG. 1. Average number of birds/stop on 198 Breeding Bird Survey transects (1985–1994). Bold lines in panels A–D and F indicate estimated edge of range and extent of transects used in analyses. The "natural-breaks" method (ArcView) was used to identify appropriate breaks between classes (represented by differentially shaded symbols) using Jenk's optimization, which minimizes sum of variances within classes. Values are average abundances for complete routes (i.e., 50-stop segments).

puted to quantify landscape structure; they were not highly redundant and represented characteristics we deemed potentially relevant to birds. We also computed patch density and percent of landscape for each segment in each transect for each of the six cover types.

Area-weighted mean patch fractal dimension (*AWMPFD*; hereafter referred to as frac-

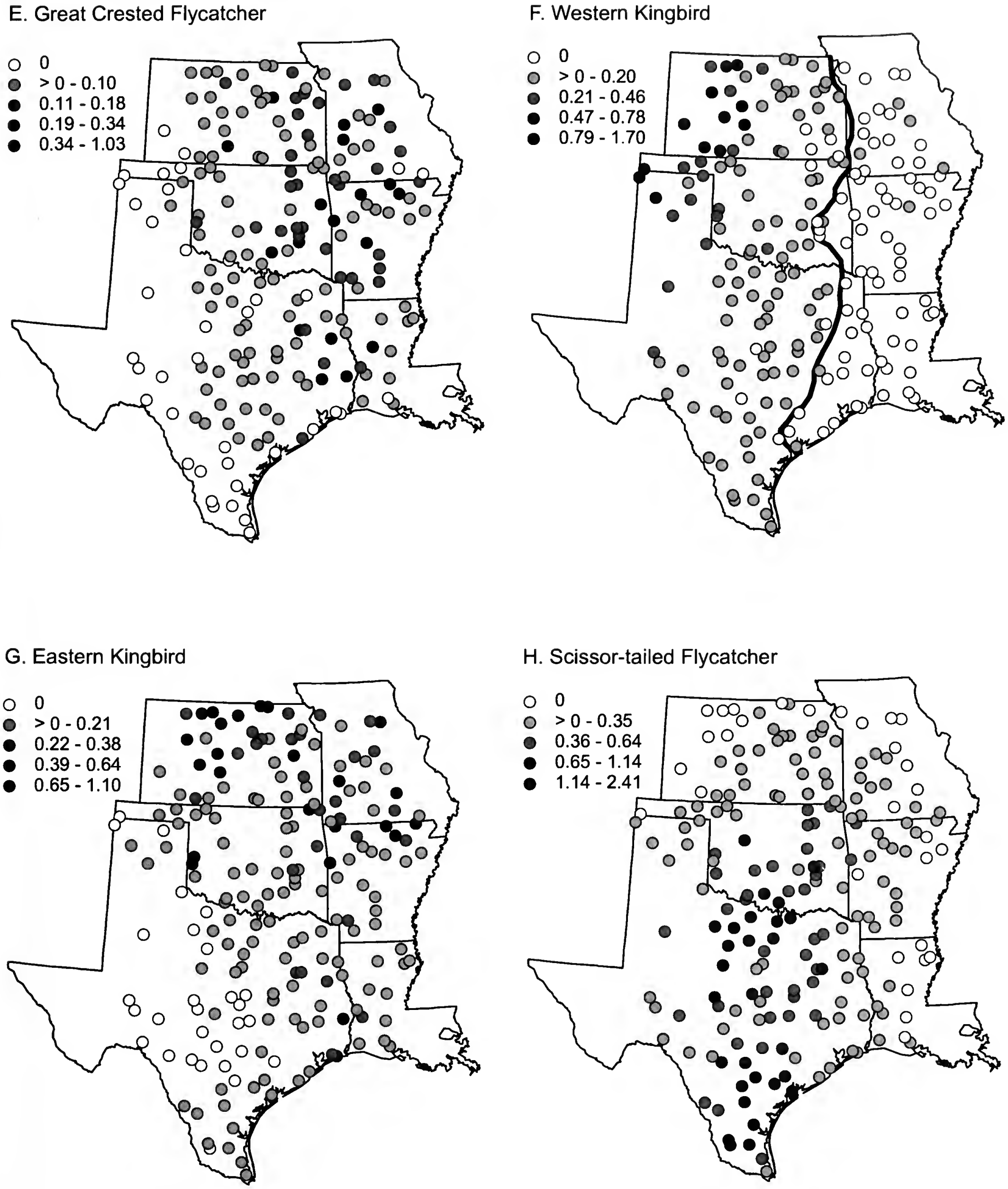

FIG. 1. Continued.

tal dimension) is a dimensionless value and was calculated using the formula

$$AWMPFD = \sum_{i=1}^{m} \sum_{j=1}^{n} \{[2 \ln(0.25 p_{ij})]/(\ln a_{ij})(a_{ij}/A)\},$$

where i is a given cover type, j is a given patch within cover type i, m is the total number of cover types (in our case, 6), n is the total number of patches within cover type i, p_{ij} is the perimeter (m) of patch ij, a_{ij} is the area (m^2) of patch ij, and A is the total area (m^2) of the landscape (in our case that of the particular segment being evaluated). This fractal-dimension index measures shape complexity of habitat patches weighted by the area of each patch. Higher values for fractal dimension indicate greater shape complexity.

Edge density (*ED*; m/ha) indicates the amount of edge per unit area and was calculated as

$$ED = 10{,}000E/A,$$

where E is the total edge (m) of the segment minus the boundary and A is the total area (m^2) of the segment.

Patch density (*PD*; number/100 ha), for the total number of patches and the number of each cover type, can be used as a measure of spatial heterogeneity within a landscape with higher values indicating greater spatial heterogeneity. It was calculated as

$$PD = (10{,}000)(100)N/A \quad \text{or}$$
$$(10{,}000)(100)n_i/A,$$

where N is the total number of patches, A (m^2) is the total area, and n_i is the total number of patches of cover type i in the segment.

Percentage of landscape (*%LAND*) is a measure of landscape composition; in this case it represents how much of the landscape is comprised of each particular cover type. We used the formula

$$\%LAND = 100 \sum_{j=1}^{n} a_{ij}/A,$$

where n is the total number of patches of cover type i, a_{ij} is the area (m^2) of patch j of cover type i, and A is the total area (m^2) of the segment.

Statistical Analysis.—Ten landscape variables (Table 2) were quantified that involved two measures encompassing five cover types (urban, closed forest, open forest, open country, and water). We used principal components analysis (PCA) to reduce the number of variables to be analyzed and consider that many of the 10 variables are intercorrelated. Thus, we were able to produce an interpretable, reduced set of composite landscape variables that are orthogonal (i.e., uncorrelated). The sixth cover type, bare ground, was not used in the PCA; bare ground was present along only a few transects and, because of the method of standardization, would have inordinately affected the values of component scores for those transects. Principal components analysis was performed using NTSYS-pc (Rohlf 2003).

TABLE 2. Loadings (correlations) of 10 landscape variables on principal components I and II based on 198 Breeding Bird Survey transects (50-stop segment length; i.e., complete length of route).

Variable	Principal component	
	I	II
Patch density		
Urban	0.77[a]	−0.18
Closed forest	0.87[a]	0.00
Open forest	0.90[a]	−0.04
Open country	0.87[a]	0.27
Water	0.60	−0.05
Percent of total area		
Urban	0.18	−0.05
Closed forest	0.02	0.92[a]
Open forest	−0.11	0.23
Open country	0.01	−0.98[a]
Water	0.03	0.20
Eigenvalue	3.32	2.00
Percent explained	33.2	20.0

[a] Relatively high loadings (> |0.8|).

The 10 landscape variables were standardized (mean of 0, standard deviation of 1) with the initial analysis being based on entire routes for the 198 transects. A Pearson product-moment correlation matrix among the 10 variables was created from which we extracted the first two principal components. We chose to examine the first two components because the eigenvalues began to level off at relatively low values at and beyond the third component. We obtained projections onto the components (i.e., component scores) using the matrix operation

$$\boldsymbol{P} = \boldsymbol{F}'\boldsymbol{O},$$

where $\boldsymbol{O}$ was the standardized data matrix having 10 variables and 198 transects (columns), and $\boldsymbol{F}$ was the matrix of principal component loadings of the 10 variables and two components. The projections were divided by $10^{0.5}$ to make them numerically consistent with average taxonomic distances among transects (Rohlf 2003).

We calculated projections for each of the 16 spatial scales. We used the $\boldsymbol{F}$-matrix from the analysis of all stops combined, but $\boldsymbol{O}$ was changed, basing it on the standardized landscape measures for all segments in all transects for the spatial scale being analyzed. Use of the same

F-matrix meant the same composite variable was analyzed at each scale, which would not necessarily have been the case had separate and independent principal components analyses been conducted at each scale.

Product-moment correlations also were calculated of abundances for each bird species with each of the five landscape variables (e.g., fractal dimension, edge density, total patch density, component I, and component II) at each of the 16 environmental scales. Transects were partitioned into 1 to 50 segments, a segment referring to a section containing a designated number of stops (i.e., point counts). For example, when examining a spatial scale of two stops, each transect included 25 segments. For a spatial scale of three stops, a single transect contained 16 segments; two stops remained at the end of the transect and were not used. In all cases where the transect ended with less than the designated number of stops for a segment, the stops at the end were not incorporated in the analysis. The average abundance per stop for each species was calculated for each segment for each transect. We also calculated the landscape metric for each segment of each transect.

We used resampling (Simon 1997, Blank et al. 2001), given that adjacent segments within a transect were not likely to be statistically independent, to create an appropriate distribution with which to statistically evaluate our results. Shuffling the bird-abundance data by entire transects and then by segments within the transect considered the spatial autocorrelation within transects. The order of transects was shuffled in the first iteration, but the order of segments within each transect remained constant. This resulted in the abundance data for each transect being paired randomly with the landscape data of each transect. In the second iteration, abundance data according to segment were shuffled, which resulted in bird data being paired with random landscape data by segment. Each shuffle was done without replacement. We then associated segment one of the bird-abundance data with segment one of the landscape data, segment two of the bird-abundance data with segment two of the landscape data (all within the same transect), etc., and calculated the correlation based on the paired values for each segment for all transects. We shuffled the abundance data and calculated correlation values in this manner 10,000 times. This distribution of correlations allowed us to evaluate the statistical significance of the observed correlation value. This procedure was repeated for each species at each scale, providing an appropriate series of statistical tests.

We did not attempt to interpret sets of correlations between bird abundance and particular landscape measures where all correlations were <0.15, even if some were judged to be statistically significant. Weak correlations of this magnitude statistically explain only a low percentage of the possible covariation of bird abundances and landscape variables.

RESULTS

Landscape Variables.—Fractal dimension, when evaluated for the full lengths of transects, exhibited high values in the east and central regions of the study region, and generally lower values in the west (Fig. 2A). This indicates that shapes of patches were simpler to the west. Values for edge density (Fig. 2B) were low in the west with the highest values in central and north-central areas, and moderate to low values in the east. Total patch density (Fig. 2C) was higher in the east-west transitional areas and relatively low in the east and west. Thus, transects in the central portion of the region tended to have more habitat edge and more habitat patches, whereas patches had simpler shapes in the west.

Projections on (i.e., scores for) landscape principal component I based on 10 variables showed high values in the central portion of the study region and low values in the west, and to some extent in the east (Fig. 3A). Environmental variables having the highest loadings (correlations) on component I were patch densities for urban, closed forest, open forest, and open country (Table 2). This component indicated that transects in the central part of the region had more habitat patches of these four cover types than transects in the east and especially the west. Component I projections closely paralleled values for overall patch density for 50-stop segments, (Figs. 2C, 3A).

Landscape component II showed clinal variation from high values in the east-central portion of the region to low values in the northwest (Fig. 3B). This component had a high positive loading with percent area of closed

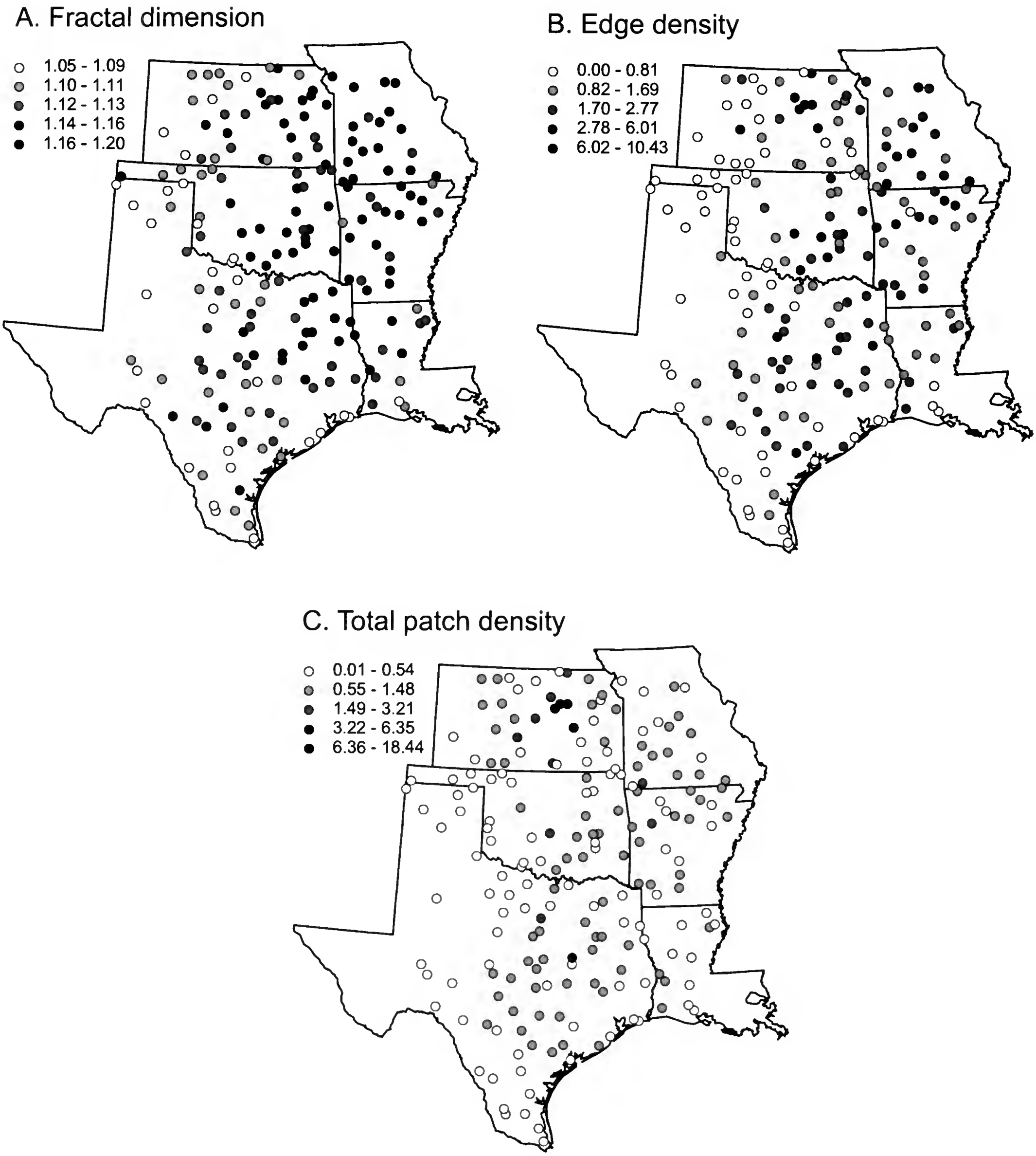

FIG. 2. Fractal dimension, edge density (m/ha), and total patch density (patches/100 ha) based on 198 Breeding Bird Survey transects. The "natural-breaks" method was used to identify appropriate breaks between classes with classes being represented by differentially shaded symbols. Values are those for complete routes (i.e., 50-stop segments). Patterns at times varied from these when considering other scales.

forest and a high negative correlation with percent area of open country (Table 2). More closed forest and less open country occurred in the east-central part of the study region with the converse being true in the northwest.

Species/Landscape Trends over Various Scales.—Statistically significant relationships ($P < 0.05$) between bird abundance and landscape variables were found for fractal dimension, edge density, and component II. The other two variables, total patch density and component I, had only weak associations with bird abundances and are not considered further.

Eastern Wood-Pewees, Eastern Phoebes,

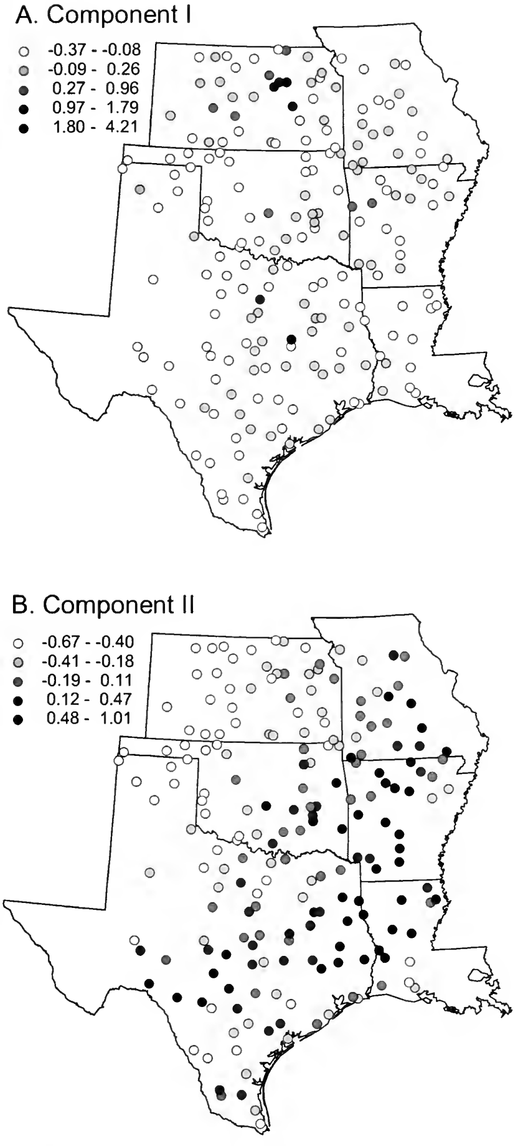

FIG. 3. Projections of transects onto principal components I and II based on 10 landscape variables measured for total length of survey route (i.e., 50-stop segment). The "natural-breaks" method was used to identify appropriate breaks between classes with classes being represented by differentially shaded symbols. Values are those for complete routes (i.e., 50-stop segments). Patterns at times varied from these when considering other scales.

and Great Crested Flycatchers had similar relationships for fractal dimension (Fig. 4). All three species exhibited correlations that increased from 1- to 25-stop segments and thereafter remained relatively constant. Western Kingbird abundance was negatively correlated with fractal dimension increasing from 1- to 12-stop segments after which values decreased. Correlations for the Scissor-tailed Flycatcher were negative and nonsignificant except at the largest scale. The highest correlations for Eastern Wood-Pewees, Eastern Phoebes, and Great Crested Flycatchers occurred at 25-, 22-, and 50-stop segments, respectively, although often correlations at adjacent scales were similar. The abundances of these species were not particularly related to fractal dimension as measured at the smaller scales where correlations, while being statistically significant, were weak. The similarities (when considering entire routes; i.e., 50-stop segments) of the geographic distribution patterns of fractal dimension (Fig. 2A) with those of the abundances of Eastern Wood-Pewees, Eastern Phoebes, and Great Crested Flycatchers (Fig. 1A, C, and E, respectively) are evident. There was a relatively strong statistical relationship with fractal dimension for three species—Eastern Wood-Pewee, Eastern Phoebe, and Western Kingbird—even with numerous study localities outside their respective ranges being excluded from the correlation analysis (Fig. 1A, C, and F).

Correlations of edge density and abundance of Eastern Phoebes tended to increase from the smallest spatial scale analyzed (1-stop segments) to the largest (50-stop segments) with a decrease in values from 17 to 25 stops (Fig. 5). The Great Crested Flycatcher had a similar pattern initially but the curve asymptotes at 17-stop segments. The relationship of Western Kingbird abundance to edge density mirrored that of the Eastern Phoebe, but with a relatively weak, negative instead of positive association.

The general correlation patterns of component II with abundances of Acadian Flycatchers, Eastern Phoebes, and Great Crested Flycatchers were similar for the range of segment lengths (Fig. 6), although the actual correlation values were different. Correlations for these species generally increased from the smallest to the largest spatial scale. The correlation of Eastern Wood-Pewee abundance with component II increased until 17-stop segments after which values leveled off and then decreased (Fig. 6). Correlations for Western

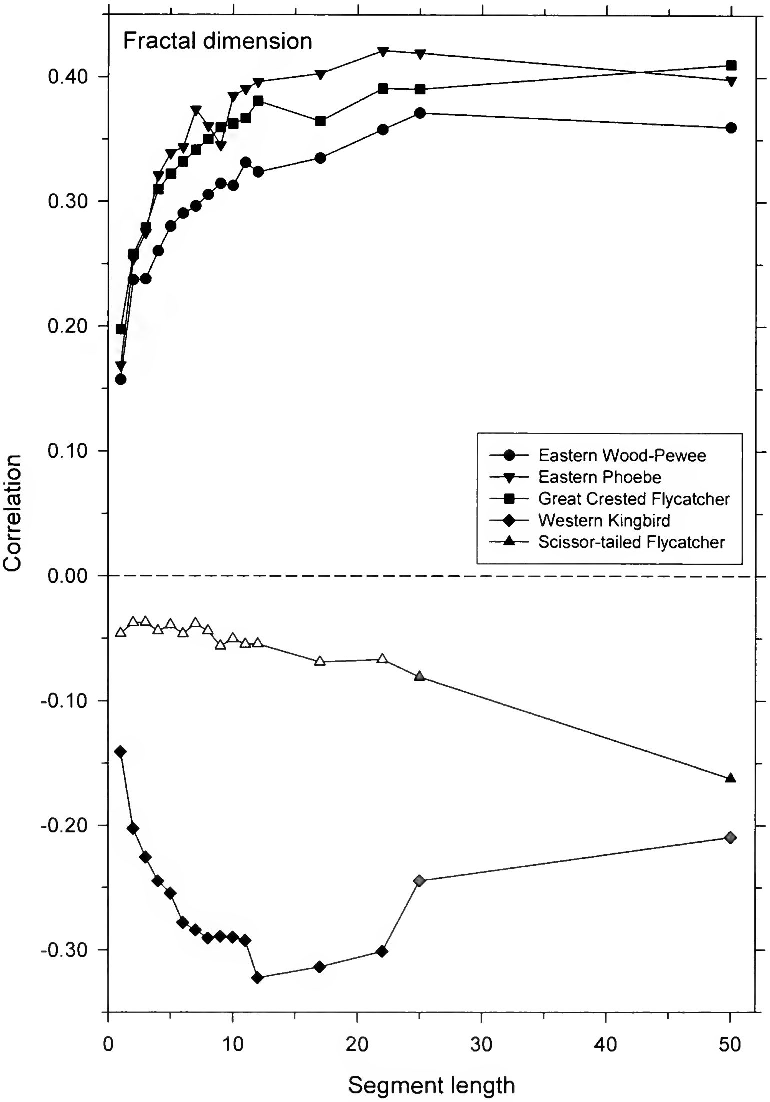

FIG. 4. Correlations over range of segment lengths of fractal dimension with average number of birds/stop for five species. Open symbols indicate nonsignificant values ($P > 0.05$), gray symbols significant values ($P < 0.05$), and black symbols highly significant values ($P < 0.01$).

Kingbirds had a similar pattern but were negative (Fig. 6). The relationship between Eastern Kingbird abundance and component II was also negative, but the association was weak and leveled off at about segment length 11 (Fig. 6). The Vermilion Flycatcher had the most restricted range within our study region and correlations were positive, increasing to a high at segment length 22 and decreasing thereafter. This association reflects that the Vermilion Flycatcher tended to be most dense (Fig. 1D) in places with relatively little of the open-country cover type. The negative correlation values for Scissor-tailed Flycatcher abundance and component II increased until segment length 3, where the curve asymptotes and correlations decreased slightly (Fig. 6); all correlations involving this species were weak.

Scale of Associations of Landscape Variables with Bird Abundances.—There were 16 sets of associations with statistically significant correlations (Figs. 4–6). The highest cor-

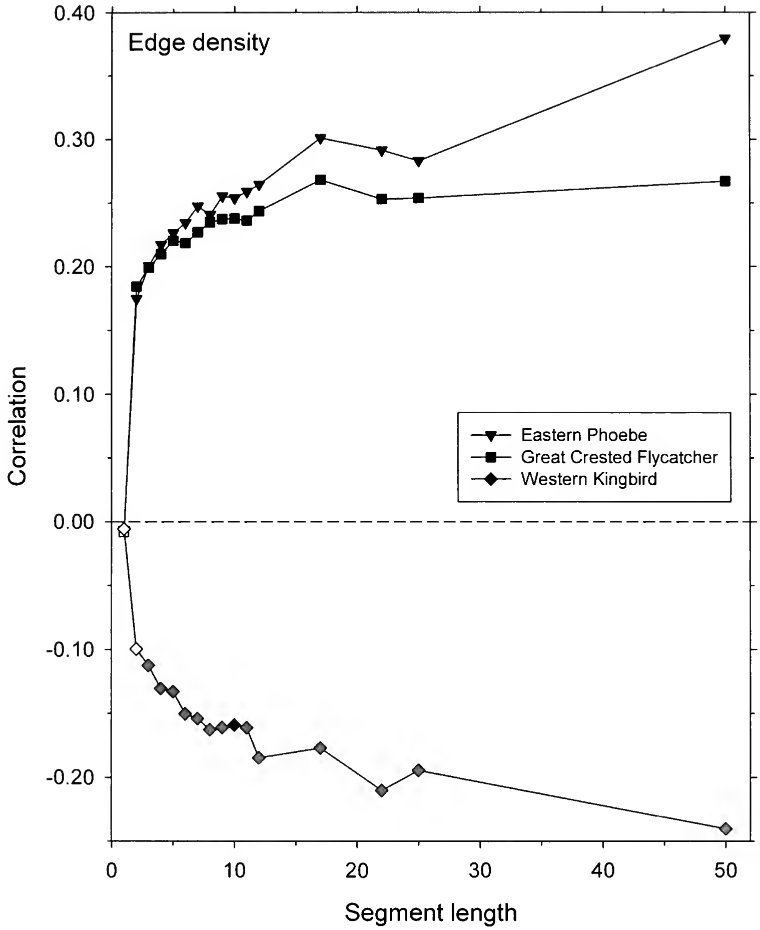

FIG. 5. Correlations over range of segment lengths of edge density with average number of birds/stop for three species. Open symbols indicate nonsignificant values ($P > 0.05$), gray symbols significant values ($P < 0.05$), and black symbols highly significant values ($P < 0.01$).

relation for six of these was at the largest scale (50-stop segments), while for seven the highest correlations were at intermediate scales (i.e., 17-, 22-, or 25-stop segments). Two had the highest correlation at shorter segment lengths.

Great Crested Flycatchers and Scissor-tailed Flycatchers had the highest correlation with fractal dimension at the largest scale (Fig. 4). Eastern Wood-Pewees and Eastern Phoebes had the greatest correlation at 25- and 22-stop segments, respectively, to fractal dimension whereas Western Kingbirds had an asymptote at a smaller spatial scale (12-stop segments).

The highest correlation of bird abundance with edge density was at the largest spatial scale (50-stop segments) for two species—Eastern Phoebe and Western Kingbird (Fig. 5). The strongest correlation for the Great Crested Flycatcher was for segment length 17.

The highest correlations with component II also occurred at the largest scale (50-stop segments) for Acadian Flycatchers, Eastern Phoebes, and Great Crested Flycatchers. The closest association occurred at an intermediate scale for Eastern Wood-Pewees, Western Kingbirds, and Eastern Kingbirds (17-stop segments; Fig. 6).

Consistency of Associations of Landscape Variables with Bird Abundances.—Only two of the eight landscape variables we investigated—fractal dimension and principal component II—had four or more species signifi-

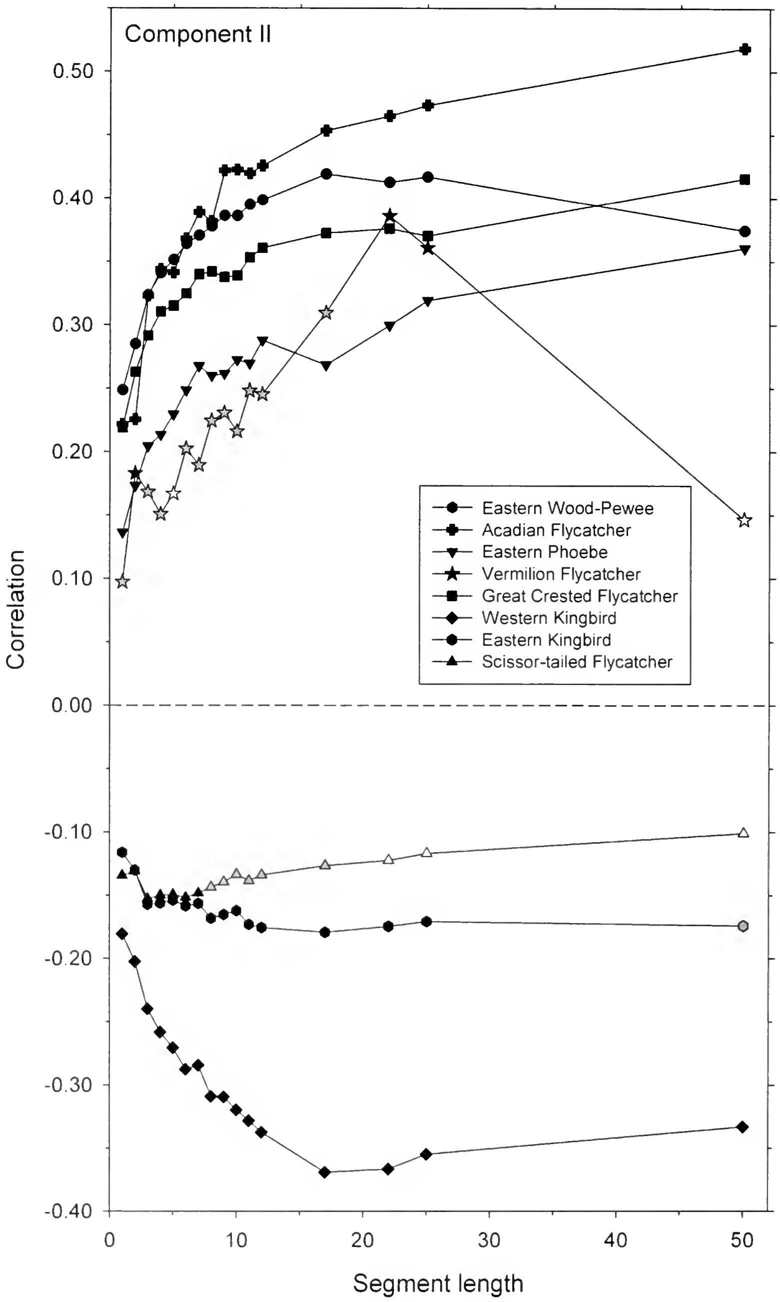

FIG. 6. Correlations over range of segment lengths of landscape principal component II (for which high values indicate closed forest and low values open country) and average number of birds/stop for eight species. Open symbols indicate nonsignificant values ($P > 0.05$), gray symbols significant values ($P < 0.05$), and black symbols highly significant values ($P < 0.01$).

cantly associated at a majority of spatial scales. Abundances of Eastern Wood-Pewee, Eastern Phoebe, Great Crested Flycatcher, and Western Kingbird were significantly associated with fractal dimension at all spatial scales (Fig. 4), and abundances of all eight tyrannids were strongly associated with component II (Fig. 6).

DISCUSSION

Species/Landscape Trends over Various Scales.—The relationship between landscape variables and species abundances was dependent on the spatial scale analyzed. Correlations generally started to level off at or near segment length 10 and were most often highest at the larger spatial scales studied (17- to 50-stop segments). Associations changed gradually with small changes in scale. There was little indication in our findings for the eight species and five landscape variables of any abrupt change in strength of associations with small changes in scale.

Studies that use a single scale (e.g., McGarigal and McComb 1995, Drolet et al. 1999) show relationships to certain environmental measures but might not be conducted at the most appropriate scale relative to other potentially important variables. In addition, it is difficult to compare studies done at different scales, given that relationships of relevant variables often change, albeit gradually, with scale. Analyzing two (typically termed coarse and fine, or broad and narrow) or three spatial scales (microhabitat, intermediate, and landscape levels; Saab 1999, MacFaden and Capen 2002) can provide a more complete picture. However, these analyses may be interpreted as implying the presence of distinctive differences in associations of environmental variables with abundances for different scales when, based on our results, it appears that typically the strengths of such associations change only gradually with incremental scale changes.

Initially we predicted, based on our intuition, as to how birds perceive their environment that associations for some landscape variables with abundances would be strongest at some intermediate scale with notably weaker associations at both smaller and larger scales. The only relationship that demonstrated this type of pattern involved correlations between Vermilion Flycatcher abundances and landscape principal component II. In most cases the highest correlations were at the larger scales, although often there was relatively little change in associations from intermediate to the largest scales.

Scale of Associations of Landscape Variables with Bird Abundances.—The scale at which landscape variables had the closest association with bird abundances depended both on the species and the variable. Correlations generally were greater at the larger spatial scales (17- to 50-stop segments). Breeding-habitat requirements are known to vary among species, but a particular variable might be more important relative to others when birds of a given species choose a suitable area.

Our study suggests that for the bird species studied, responses to the environment primarily occur at relatively large spatial scales. Spatial scale also was shown to have an effect on species richness of both butterflies and birds with larger scales having a significant effect on avian richness (Fleishman et al. 2003). Fuhlendorf et al. (2002) found that large spatial scales most often were associated with changes in species populations. In our study, bird population numbers were most closely related to landscape variables at larger spatial scales indicating that broad-scale landscape characteristics influence species abundance. However, in some instances correlations also were relatively high at smaller scales, implying that some environmental variables influence populations at a more local level.

The bird species we studied may react initially to the landscape at a regional scale, because at this level environmental factors such as those subsumed in the variables fractal dimension and component II (the amount of closed forest vs. open country) represent broad aspects of what is appropriate habitat. Nest sites may be selected in areas exhibiting these basic characteristics reflecting perception and response to local-level factors such as prey abundance, distance from habitat edge, or vegetation structure. This general characterization is related to those put forth by Hutto (1985) for habitat selection by nonbreeding, migratory birds and by Johnson (1980) for general habitat selection.

It is important to consider the species and the question being asked when deciding on the

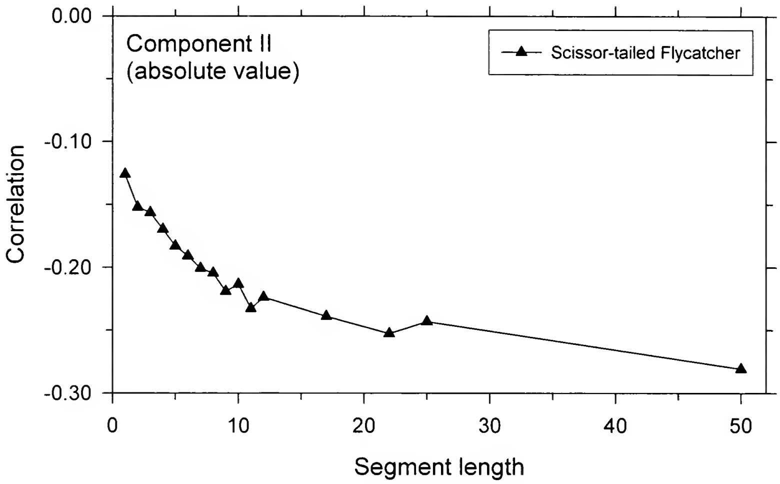

FIG. 7. Correlations over range of segment lengths of absolute values of landscape principal component II (using absolute numbers, high values indicate closed forest or open country, and low values reflect intermediate conditions such as savannah) and average number of Scissor-tailed Flycatchers/stop. All correlations were highly significant ($P < 0.01$).

scales at which to pursue particular investigations. Westphal et al. (2003) found that some species responded more to landscape metrics at a 2-km scale than at larger distance scales (5 or 10 km). Their findings and ours may indicate that a species requires a threshold amount of a particular cover type or landscape characteristic after which additional amounts are neither beneficial nor detrimental.

We examined linear relationships over the total number of transects and segment lengths, and for the complete range of a particular landscape variable. This could result in missing possible nonlinear patterns including strong associations where highest abundances occur at intermediate values for a certain landscape variable. We were analyzing transects for most of the species near either the eastern or western edge of their ranges. This may be partially responsible for the finding of substantial linear relationships between abundances and landscape variables.

The range of the Scissor-tailed Flycatcher in the United States was the initial basis for delineating the geographic limits of our study region encompassing the western, northern, and eastern extent of its range. Correlations involving abundances of this species were not above 0.20 for any of the landscape variables analyzed. Landscape component II, for example, which had values centered on zero and a general pattern extending east to west-northwest of positive-to-negative projections when considering 50-stop segments (Fig. 3B), exhibited only a weak association with Scissor-tailed Flycatcher abundance (Fig. 6). However, if one evaluates absolute values for this component, which results in the lowest values being found in the central portion of our study region with higher projection values to the west, north and east, associations of abundances and absolute component II values were significant and negative. The correlations were greatest at the largest scale studied (50-stop segments; Fig. 7). Thus, Scissor-tailed Flycatcher densities were highest in areas that were intermediate relative to the proportion of land in closed forest and open country; where closed forest became less prominent and open country more widespread, or visa versa, abundance of Scissor-tailed Flycatchers was lower. The strengths of correlations at intermediate segment lengths (17- to 25-stop segments) also suggested that extended areas of intermediate cover types, irrespective of where they occurred geographically, tended to have higher Scissor-tailed Flycatcher abundance.

Influence of Landscape Variables on Bird Abundances.—A high fractal dimension often indicates relatively undisturbed areas with complex edges whereas a low value typifies areas converted to agriculture fields, cropland, or road intersections and, thus, having more linear edges (Miller et al. 1997). The three species (Eastern Wood-Pewee, Eastern Phoebe, and Great Crested Flycatcher) showing positive correlations with fractal dimension appeared to do best in relatively undisturbed areas with comparatively high fractal dimensions. Eastern Wood-Pewees typically are found in forested areas (McCarty 1996) as are Eastern Phoebes (Weeks 1994) and Great Crested Flycatchers (Lanyon 1997). The other two species having abundances associated with fractal dimension showed a negative relationship. The Western Kingbird was strongly associated with fractal dimension and, typically, occurs in open habitats such as pastures, grasslands, and cultivated fields (Gamble and Bergin 1996), areas that have a low fractal dimension. This kingbird was more abundant in parts of our study region that were mostly open. Fractal dimension was a variable capturing the essence of an influential factor closely associated with abundances of several of the breeding species we studied.

Component II represented the percent of closed forest versus open country of an area and was significantly correlated with abundances of all eight species (Fig. 6). These associations highlight marked habitat preferences of these birds. Species that tend to occur in wooded habitats, such as Eastern Wood-Pewees, Acadian Flycatchers, Eastern Phoebes and Great Crested Flycatchers (Weeks 1994, McCarty 1996, Lanyon 1997, Whitehead and Taylor 2002), had a relatively strong positive association to component II. Our results showed population numbers of these species tended to be higher in densely wooded areas and lower in more sparsely wooded locations.

The Vermilion Flycatcher, which typically occurs in farmlands, savannahs, cultivated fields, and riparian woodlands (Wolf and Jones 2000), exhibited a weak, positive association with component II. This species was limited to the southwestern part of our study region (Fig. 1D) where it occurred mainly on transects with high scores on component II, indicating relatively closed habitat. Our experience and the literature (Wolf and Jones 2000) suggest that Vermilion Flycatchers often were associated with open spaces within closed habitat at these sites.

Birds such as Western Kingbirds, Eastern Kingbirds, and Scissor-tailed Flycatchers, which are associated with open country and savannah (Gamble and Bergin 1996, Murphy 1996, Regosin 1998), had a negative relationship with component II. Most of the birds we studied are primarily open-country or closed-forest species. Overall, component II includes some of the most important habitat factors influencing the range limits, distributions, and abundances of many of the flycatchers examined.

There can be fundamental differences in the relative influences of various environmental factors at different scales; some of these factors may be operative at one scale but not another (Saab 1999, Bergin et al. 2000, Fuhlendorf et al. 2002, MacFaden and Capen 2002). However, this does not negate the observation that in almost all cases only minor changes in association of bird abundances and landscape variables were found with small changes in scale. Hecnar and M'Closkey (1997) showed the status of the green frog (*Rana clamitans melanota*) to be scale dependent; they evaluated factors such as occupancy, abundance, and turnover at a local, subregional, regional, and geographic scale. At smaller scales, populations of green frogs were dynamic, whereas at a geographic scale it was common and stable, illustrating the importance of investigating processes at multiple scales.

Similarly, Schooley and Wiens (2001) demonstrated that dispersion of banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds were scale sensitive. They found mounds to be either regular or random at small scales, aggregated or random at intermediate scales, and aggregated at large scales. For this reason, it is important to decide on an appropriate scale(s) for a study considering both the question and the species (Wiens 1989b).

Studying and understanding the relationship between landscape variables and bird abundances at multiple environmental scales would benefit conservation efforts (Bergin et al. 2000, MacFaden and Capen 2002). For species of special concern, such as the Lesser Prairie-chicken (*Tympanuchus pallidicinctus*), studies at a small scale indicated that edge density and patch size were the only important variables whereas large-scale analysis suggested general landscape changes were most influential (Fuhlendorf et al. 2002). A multiscale approach can be helpful in examining how certain factors affect populations and can provide an objective approach to selecting the scale or scales most relevant to a particular study. Once these cogent variables are ascertained, conservation strategies that consider scale can be implemented to best protect relevant habitats and species.

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THE INFLUENCE OF INTERSPERSION ON MARSH BIRD ABUNDANCE IN NEW YORK

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ABSTRACT.—Interspersion is a key habitat component related to marsh bird abundance, but is not easily quantified. We used Fragstats 3.3 and aerial photos to measure interspersion within wetlands as m/ha of interface between vegetation and water (i.e., edge density). We then related edge density and other factors (marsh area, cover-to-water ratios, marsh area within 5 km) to the abundance of marsh birds on 16 emergent wetlands in New York during 2005. Abundance was assessed via call broadcast surveys for American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), Pied-billed Grebe (*Podilymbus podiceps*), Sora (*Porzana carolina*), and Virginia Rail (*Rallus limicola*). Interspersion, as measured by edge density, was the best predictor of abundance for all species but Pied-billed Grebe (r^2 = 0.30–0.71). Vegetation and water interspersed in a spatially complex pattern likely increases breeding diversity and density of marsh birds. Modern spatial analysis programs provide opportunities to quantify interspersion without intensive field work or calculations, which can lead to more accurate research and management efforts focused on marsh birds. *Received 11 May 2006. Accepted 1 December 2006.*

Major wetland loss over the past two centuries in the United States has caused declines in marsh birds; hence, there is increasing pressure on extant wetlands to support and maintain their populations (Tate 1986, Eddleman et al. 1988, Conway et al. 1994). Many factors affect marsh bird abundance and overall wetland bird diversity (e.g., marsh size and isolation; Brown and Dinsmore 1986, Gibbs et al. 1991, Grover and Baldassarre 1995), but the abundance of wetland birds is especially high on wetlands characterized as "hemi-marsh" (Weller and Spatcher 1965, Weller and Frederickson 1974, Gibbs et al. 1991, Murkin et al. 1997). Weller and Spatcher (1965) first described hemi-marsh as that with an equal proportion (50:50) of emergent cover and open water (cover-to-water ratios) distributed in an "interspersed" pattern. However, while definitions and measurements of marsh size and isolation are self evident, interspersion is not.

Kaminski and Prince (1981) created a 1:1 cover-to-water ratio by mowing five, 0.1-ha circles in a contiguous 1-ha stand of mixed-emergent vegetation. This ratio also could be created by mowing half the vegetation in a more complex pattern of smaller patches, thus, increasing interspersion. Similarly, Murkin et al. (1982) and Smith et al. (2004) used mowing to create plots with varying cover-to-water ratios on which they measured response by waterbirds, but not actual interspersion. Lack of this measurement is significant because many configurations of emergent vegetation and open water can yield "hemi-marsh," yet permutations could be vastly different in terms of interspersion. Interspersion, therefore, could be a strong explanatory variable affecting marsh bird abundance relationships occurring within hemi-marshes, but this component of wetland habitat has gone unmeasured except for a complicated approach used by Gibbs et al. (1991) and a labor intensive approach used by Murkin et al. (1997).

We believe interspersion is the amount of mixing that occurs between the two major marsh cover types, vegetation and water. Thus, a quantitative measure of interspersion would be the amount (m/ha) of interface between vegetation and water (i.e., edge density or ED), because edge will increase in direct proportion to mixing. Furthermore, the quantitative nature of the ED measurement allows an easy and precise comparison of interspersion among marshes of varying size (McGarigal and Marks 1995). We were especially interested in ED because modern spatial analysis programs such as Fragstats 3.3 (McGarigal et al. 2002) easily provide ED measurements, which reduce the need for intensive fieldwork or complex calculations. Our objective was to quantify and relate interspersion (i.e., ED) to the abundance of marsh birds

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using emergent wetlands in New York; we were secondarily interested in the influence of marsh size, isolation, and cover-to-water ratios.

METHODS

We sampled 16 emergent wetlands for marsh birds in 2005 in two ecozones in New York: the Great Lakes Plain in western and central New York, and the St. Lawrence Plains in northern New York (Andrle and Carroll 1988). Wetlands surveyed in west-central and northern New York included the French Creek Wildlife Management Area (WMA; 2 sites, 7.7 and 130 ha), Cranberry Creek WMA (2 sites, 36.0 and 68.4 ha), Crooked Creek Nature Preserve (2 sites, 11.2 and 238 ha), the Oak Orchard/Tonawanda/Iroquois wetland complex (8,000 ha) (7 sites, 20.0–155 ha), Lakeview WMA (1 site, 774 ha), Cayuga Lake WMA (1 site, 91.0 ha), and a privately owned marsh (Vailis, 3 ha) adjacent to Montezuma National Wildlife Refuge.

Spatial arrangement of vegetation and open water varied substantially among study sites, which presented a wide range of interspersion values. Emergent vegetation of all marshes was dominated (>60%) by cattails (*Typha* spp.). Water control structures were present on 10 of the 16 wetlands, which permitted varying levels of habitat manipulation. Rehm (2006) provides a detailed description of each study wetland.

We conducted unlimited-radius point counts coupled with call broadcast periods for five target marsh birds: Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), Virginia Rail (*Rallus limicola*), and Sora (*Porzana carolina*) (Conway 2005). We mapped all potential survey points at each marsh, following a modified version of the national protocol, which recommends spacing points at 400-m intervals (Conway 2005). We spaced points at 200-m intervals to (1) allow more points in small marshes, and (2) facilitate detection of Least Bittern, Virginia Rail, and Sora, which have a detection limit within 100 m of the observer (Gibbs and Melvin 1993). We placed the first sample point along the marsh–open water interface, 200 m from our canoe launch point, and then mapped all potential survey points at 200-m intervals along that interface. We placed points in the interior of large cattail stands and along the upland edge when sampling from the marsh–open water interface could not provide adequate survey coverage within a given wetland. We calculated the maximum number of points we could survey over the sampling period and allocated those points to each marsh based on marsh size (i.e., more points in larger marshes). We used a stratified random sampling approach to ensure survey points were evenly dispersed within each marsh. Initial location of points was done with Geographic Positioning System (GPS) units and Universal Transverse Mercator (UTM) coordinates from aerial photos. Points were marked with temporary flagging and mapped on an aerial photo to aid in relocation.

We conducted surveys at 143 points on 16 marshes from 11 April to 8 July 2005. Marshes were surveyed between 30 min before and 4.5 hrs after sunrise (Gibbs and Melvin 1993). Each point was surveyed four times and surveys were separated by at least 7 days (Conway 2005). Surveys were not conducted during periods of precipitation or wind speeds >20 km/hr (Gibbs and Melvin 1993).

We used a 10-min survey with a 3-min passive listening period before a 7-min broadcast of calls. The calls consisted of territorial calls broadcast in the order of Least Bittern, Sora, Virginia Rail, American Bittern, and Pied-billed Grebe. All calls were from the Peterson's Field Guide CDs (Walton and Lawson 1994). A 30-sec call was broadcast once for each species, followed by 30 sec of silence, except for Least Bittern. Two additional Least Bittern call periods were added to the beginning of the broadcast period because their detection rates can increase with the length and number of call periods (Bogner and Baldassarre 2002a).

Calls were broadcast at 80–90 dB, 1 m from four speakers arranged at 360°. In the canoe, speakers were mounted on a board laid across the bow; on land, speakers were held at chest height and pointed towards the marsh. At each survey station, we recorded all birds seen or heard, when detection occurred (e.g., passive listening, Least Bittern broadcast period, etc.), and spot-mapped all individuals detected to reduce the probability of double-counting.

We measured habitat variables for all marshes from 0.61-m (2-ft) color infrared or black and white panchromatic aerial photos obtained from the New York State GIS Clearinghouse. All photos were taken in April or May 2002 or 2003. Each photo was edited wherein only the marsh area was visible and corrected for any photo imperfections (e.g., shadows). We surveyed all areas of each marsh from a canoe in April and May 2005 to ensure inclusion of any emergent vegetation or open water, and to record any changes in marsh structure that occurred since photos were taken (2002–2003) and our study (2005). We classified the photo pixels into two classes (water and vegetation) using a supervised classification command in program IDRISI (Clarks Lab 2003). All emergent vegetation was categorized as one class because we wanted to analyze effects of interspersion of water and vegetation on bird use, not the response to variation in types of emergent vegetation. A supervised classification was necessary due to variation in photograph color and year. During a supervised classification, we "trained" the computer to recognize the values of infrared light reflectivity for each class (water or vegetation) based on pixel values at defined training sites. Two training sites (water and vegetation) were used for each individual photo, and training sites consisted of at least 1,000 pixels per class. Training sites with selected pixels were field-checked or verified from aerial photos and entered into the computer as one of the two classes. The computer assigned all remaining pixels to one of the two classes based on the values defined by the training sites.

Classified images were analyzed in Fragstats 3.3 (McGarigal et al. 2002) to obtain values for marsh size (AREA), cover-to-water ratios (RATIO), and ED. We used aerial photographs and the buffer command in ArcGIS (ESRI 2005) to measure area of marsh within 5 km (5KM) from the center of each study wetland. We assumed that AREA, ED, and 5KM were linearly related to marsh bird abundance. However, RATIO is not linearly related to marsh bird abundance because marsh birds prefer habitats with 50:50 cover-to-water ratios and avoid areas with 100% water or 100% vegetation (Weller and Spatcher 1965, Weller and Frederickson 1974, Gibbs et al. 1991, Murkin et al. 1997). We calculated percent water on each marsh, subtracted that value from 50, and multiplied the absolute value by two to obtain a RATIO measurement linearly related to marsh bird abundance. Consequently, wetlands with cover-to-water ratios approaching 1:1 (50% water, 50% cover) were given values close to 0, and wetlands moving away from 1:1 ratios (e.g., 0 or 100% water) were given values closer to 1.

Relative abundance for each target species was calculated as the average number of birds per point at each marsh. We chose to calculate relative abundance as birds per point and not birds/ha, because we used an unlimited-radius point count as recommended by established protocols (Conway 2005). However, the unlimited-radius count creates variation in area surveyed per point, depending on the shape of each marsh and the characteristics of adjacent uplands. In addition, we did not have complete survey coverage of all marshes.

We used forward stepwise multiple regression ($\alpha = 0.05$ for entry) (Zar 1999) to generate a model of relative abundance of marsh birds using the predictor variables AREA, ED, 5KM, and RATIO. We used Pearson's correlation analysis to detect any relationships not found via the regression models, and to quantify the association between habitat variables and relative bird abundance. Correlation values ($\alpha = 0.05$) between habitat variables were examined to test for autocorrelation and interaction among predictor variables. All analyses were completed in Minitab (Minitab Inc. 2005). All means are reported as ± standard error.

RESULTS

We conducted 572 surveys at 143 survey points on 16 marshes and recorded 663 detections of target species: 213 Virginia Rails (32%), 179 American Bitterns (27%), 153 Pied-billed Grebes (23%), 76 Least Bitterns (12%), and 42 Soras (6%). Only American Bitterns were detected at all marshes, although Virginia Rails were detected at all but one marsh. Pied-billed Grebes were detected at eight marshes, seven of which were at the Oak Orchard/Tonawanda/ Iroquois wetland complex. The Virginia Rail had the highest relative abundance (0.54 ± 0.11 birds/point), whereas Sora had the lowest (0.1 ± 0.04

TABLE 1. Forward step-wise (α for entry = 0.05) regression models of four habitat variables (marsh area, edge density, area of marsh within 5 km, and cover-to-water ratios) as predictors of marsh bird relative abundance (birds/point) at 16 wetlands in New York State, 2005.

Bird variable	Components[a] in model	r^2
American Bittern	−0.1208 + 0.0002 ED*	0.43
Least Bittern	−0.0260 + 0.0002 ED*	0.30
Pied-billed Grebe	0.2567 + 0.0002 5KM − 0.79 RATIO	0.72
Sora	−0.0691 + 0.0002 ED*	0.38
Virginia Rail	0.0363 + 0.0007 ED* − 0.0002 5KM*	0.71

[a] ED = Edge Density (m/ha); RATIO = cover-to-water ratio; 5KM = area of within 5 km of target wetland (ha).
* $P < 0.05$.

birds/point). Abundance values were 0.35 ± 0.11 for Pied-billed Grebe, 0.34 ± 0.04 for American Bittern, and 0.19 ± 0.05 for Least Bittern.

Average AREA across all wetlands was 116 ± 46 ha (range = 8–774 ha), ED was 1,124 ± 147 m/ha (range = 204–1,970), 5KM was 2,035 ± 283 ha (range = 609–3,424), and the transformed RATIO was 0.43 ± 0.07 (range = 0.06–0.80). Regression analysis yielded significant single or multivariable models to predict relative abundance of marsh birds of which three of four independent variables (ED, RATIO, and 5KM) were included in the models (Table 1). AREA was the only independent variable excluded from all models. ED was positively related to relative abundance of American Bittern, Least Bittern, and Sora in single-variable models (r^2 = 0.30–0.43; Table 1). The relative abundance of Virginia Rail also was positively related to ED but in a two-variable model that included 5KM (r^2 = 0.71). The Pied-billed Grebe was the only species not related to ED in any model. However, Pied-billed Grebe abundance was positively correlated with ED (r = 0.61), which was the only correlation between habitat variables and bird abundance not included in the regression models (Table 2).

DISCUSSION

Edge density, which indicates interspersion and is easily measured via Fragstats, was an important habitat variable affecting secretive marsh birds in our study as reflected by its inclusion in four of five regression models (all but Pied-billed Grebe). Increased interspersion is synonymous with increased ED and is of known importance to several species of marsh birds. In Maine, for example, American Bitterns were found on wetlands with extensive interspersion (Gibbs et al. 1991); in Iowa, Least Bitterns avoided areas with dense emergent vegetation until muskrats (*Ondatra zibethicus*) created openings (Weller and Spatcher 1965). Additionally, both American and Least bitterns feed along the vegetation–water interface in the interior of wetlands (Weller 1961; Gibbs et al. 1992a, 1992b). Least Bittern nests also occur within 3.5–10.0 m of open water (Gibbs et al. 1992b, Bogner and Baldassarre 2002b). Similarly, Sora nests tend to occur at edges between different vegetation types or between vegetation and open

TABLE 2. Pearson's correlation coefficients of four habitat variables[a] (marsh area, edge density, area of marsh within 5 km, and cover-to-water ratios) and relative bird abundance (birds/ha) at wetlands in New York State, 2005.

Variable	American Bittern	Least Bittern	Pied-billed Grebe	Sora	Virginia Rail
5KM	0.29	0.03	0.75*	0.18	0.14
RATIO	−0.41	−0.10	−0.71*	−0.16	−0.23
ED	0.65*	0.55*	0.61*	0.62*	0.77*
AREA	−0.19	−0.30	−0.22	−0.27	−0.42

[a] 5KM = area of marsh within 5 km of target wetland (ha); ED = Edge Density (m/ha); RATIO = cover-to-water ratio; and AREA = marsh size (ha).
* $P < 0.05$.

water (Walkinshaw 1940, Glahn 1974); hence more edge increases possible nesting sites.

Interspersion might also promote visual isolation, which Murkin et al. (1982) suggested may have decreased intraspecific competition and increased breeding waterfowl pair densities in Manitoba, Canada. Perhaps visual isolation affected marsh bird densities, because all targeted species in our study exhibit aggressive intraspecific territorial defense during breeding (Gibbs et al. 1992a, 1992b; Conway 1995, Melvin and Gibbs 1996, Muller and Storer 1999); only the Least Bittern occasionally nests semi-colonially (Weller 1961, Kushlan 1973). In addition to intraspecific competition, Sora and Virginia Rail also exhibit interspecific territory defense during breeding (Kaufmann 1983, 1989). Sora and Virginia Rail frequently vocalized and/or approached the speakers during our study in response to interspecific playback (i.e., Sora responded to calls of Virginia Rails). Therefore, well-interspersed vegetation and water in a spatially complex pattern may reduce inter- and intraspecific confrontations and result in increased breeding densities of these species on hemi-marshes.

Virginia Rail abundance was also related to ED but in a two-variable model negatively related to 5KM. However, ED alone was highly correlated with Virginia Rail abundance (r = 0.71), versus 0.14 for 5KM, and 0.42 for AREA. Area and area-related measurements (i.e., 5KM) may be unlikely predictors of Virginia Rail abundance because this species is a wetland generalist, and home range during breeding is relatively small (<2.0 ha) (Conway 1995). Conversely, ED is an important habitat variable because interspersion appears to be a major proximate factor affecting the abundance of Virginia Rails on individual wetlands (Conway 1995). Therefore, Virginia Rail may choose breeding habitat based on individual marsh characteristics (i.e., ED) and not surrounding habitat (i.e., 5KM).

ED was selected in four of the five regression models and was significantly correlated (r = 0.55–0.77) with all species (Tables 1, 2). We believe ED is an important variable influencing marsh bird abundance because ED increases as cover-to-water ratios approach 1:1 (ED and RATIO were correlated at r = 0.63). An increase in ED may be important to marsh birds because increased levels of macroinvertebrates are associated with hemi-marsh and related interspersion, which can increase marsh bird numbers (Voigts 1976, Kaminski and Prince 1981). Macroinvertebrate abundance is significant because Virginia Rails primarily feed on invertebrates and Sora greatly increase consumption of aquatic macroinvertebrates during spring (Conway 1995, Melvin and Gibbs 1996). In addition, insects comprise a large part of the diet of American and Least bitterns (Gibbs et al. 1992a, 1992b). Further, although interspersion increases as cover-to-water ratios approach 1:1, our data indicate that interspersion, as measured by ED, better explains the abundance of marsh birds than does cover-to-water ratios and is accurately and easily calculated with Fragstats software.

In contrast to ED, RATIO was included only in the Pied-billed Grebe model (Table 1) and was only significantly correlated with grebe abundance (−0.71; Table 2). The negative relationship between abundance of Pied-billed Grebes and the transformed RATIO was synonymous with increased water coverage, which is an important habitat variable for this species (Muller and Storer 1999). The 5KM and RATIO variables also were significant in a two-variable regression model for the Pied-billed Grebe (r^2 = 0.72), likely because grebes are area-dependent (Brown and Dinsmore 1986, Gibbs et al. 1991, Muller and Storer 1999). We did not detect Pied-billed Grebes on small, isolated wetlands, and there was no correlation between AREA and detection of grebes. However, except for one individual, all Pied-billed Grebes detected were at the Oak Orchard/Tonawanda/Iroquois wetland complex where many wetlands were separated by narrow dikes (<10 m wide). Hence, we were functionally sampling large marshes in the case of Pied-billed Grebes.

Pied-billed Grebe abundance was correlated with more than two habitat variables: 5KM, ED, and RATIO (Table 2). Pied-billed Grebes mainly forage underwater and rarely use vegetation and water interfaces as feeding sites (Muller and Storer 1999), which would reduce use of edge created by interspersion but obviously favor open water. Conversely, Pied-billed Grebes nest along edges of emergent vegetation, wherein proximity to open water and depth of water at nest sites are important factors in nest site selection (Glover 1953, Muller and Storer 1999). Because Pied-billed Grebes forage in the open and nest directly adjacent to open water, they may choose different habitat variables within a marsh than the other four target species. Therefore, measurements of ED and RATIO may have been important, because both could indirectly measure the number, size, and distribution of open water areas, which collectively affect habitat use by Pied-billed Grebes (Muller and Storer 1999).

CONSERVATION IMPLICATIONS

Many Great Lakes wetlands have experienced anthropogenic alterations to the hydrologic regime, which has resulted in a drastic reduction in open water and vegetative interspersion (Keddy and Reznicek 1986, Wilcox and Whillans 1995, Keough et al. 1999). These hydrologically disturbed wetlands illustrate the need for active management. On our study sites, for example, marshes with poor interspersion were generally characterized by large, thick, dry stands of cattail that impede movements of marsh birds and discourage nesting (Manci and Rusch 1988, Gibbs et al. 1991). We recommend that wetlands for marsh birds be managed to increase interspersion (i.e., ED) while maintaining cover-to-water ratios close to 1:1.

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ABUNDANCE AND DIVERSITY OF SHRUB-STEPPE BIRDS IN RELATION TO ENCROACHMENT OF PONDEROSA PINE

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ABSTRACT.—Fire suppression has resulted in a greater density of ponderosa pine (*Pinus ponderosa*) in grassland and shrub-steppe habitats potentially reducing habitat quality for declining grassland and shrub-steppe birds. Birds were surveyed at 10 shrub-steppe sites in the southern Okanagan Valley of British Columbia to examine whether encroachment of pine affected grassland and shrub-steppe birds. Encounter rates did not differ between years and were combined for a total of 4,281 sightings and 80 species. Sites with more ponderosa pine had a greater diversity of birds. Grassland and shrub-steppe birds as a group declined with increasing numbers of trees. Forest and open woodland birds increased in number as did generalist birds. These results support conservation efforts to reduce conifer densities in shrub-steppe habitats to benefit associated declining bird populations. *Received 18 December 2006. Accepted 7 February 2007.*

Woody invasions into grassland habitats have altered ecosystem characteristics across North America, and affected the bird assemblages that inhabit them (Bakker 2003). Generally, when shrubs and trees invade grassland habitats, avian diversity increases as shrub and forest birds are added to the assemblage (Coppedge et al. 2004). This is at the expense of birds associated with grasslands and, given their precipitous decline in recent decades (Sauer et al. 2005), woody invasions are of conservation concern. For example, in the mixed grass prairie of northern mid-United States, willows (*Salix* spp.) and aspen (*Populus tremuloides*) have invaded prairie habitats making them unsuitable for grassland birds (Grant et al. 2004). In the central United States, eastern red cedar (*Juniperus virginiana*) is the dominant habitat characteristic influencing the grassland bird assemblage (Chapman et al. 2004) and has contributed to their decline (Coppedge et al. 2004).

There are few data on the effect of tree encroachment on avian abundance and diversity in shrub-steppe habitats of the Intermountain West. Avian conservation issues associated with the shrub-steppe ecosystem have largely been livestock grazing (Bock et al. 1993, Saab et al. 1995), fragmentation and loss of shrub cover to agricultural activities (Vander Haegen et al. 2002, Knick et al. 2003), and range "improvements" such as planting crested wheatgrass (*Agropyron cristatum*) (Bradford et al. 1998). Invasion of cheatgrass (*Bromus tectorum*) is of particular concern, converting shrub-steppe to annual grasslands dominated by cheatgrass (Knick and Rotenberry 2000). These threats to the shrub-steppe ecosystem may have contributed to declines of the sagebrush-dependent subspecies of Brewer's Sparrow (*Spizella breweri breweri*) of 2.5% per year from 1965 through 2005 (Sauer et al. 2005).

Encroachment of a variety of juniper (*Juniperus* spp.) species (Miller and Wigand 1994) along with pinyon pine (*Pinus monophylla*) in the south (Tausch et al. 1981) and ponderosa pine (*P. ponderosa*) in the north (Miller and Rose 1999, Turner and Krannitz 2001) has been reported in shrub-steppe habitats throughout the Intermountain West, but the effect on the bird assemblage is largely unknown. Knick et al. (2003) reported that increases in trees resulting from fire suppression was the second most dominant explanatory trend in the bird data (after increasing fire frequency because of cheatgrass invasion). Thus, it is probable that tree invasion into shrub-steppe will also have a strong effect on the bird community similar to that in grassland habitats.

The objective of this study was to examine the effect of different densities of ponderosa pine in a shrub-steppe ecosystem on avian abundance, diversity, and composition in the southern Okanagan Valley, British Columbia, Canada.

METHODS

Study Area.—The Okanagan Valley in southern British Columbia, Canada, is in the rain

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shadow of the Coast and Cascade ranges and is classified as semi-desert with most precipitation in winter. The mean annual precipitation between 1971 and 2000 in the study area was 326 mm (Penticton: 332.7, Oliver: 327.5, Osoyoos: 297.2 mm; http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html).

Ecosystem classification is used commonly in British Columbia to assist with management of its diverse land base (Banner et al. 1996). Polygons of habitat in the southern Okanagan and Similkameen valleys were classified and mapped in 1991–94 by a precursor to Terrain Ecosystem Mapping (TEM) called Biophysical Mapping (Iverson and Haney 2006). I selected 24 polygons on the east side of the Okanagan Valley with the same shrub-steppe classification ("AN": antelope bitterbrush [*Purshia tridentata*] with needle-and-thread grass [*Hesperostipa comata*] and coarse textured soils) as potential sites for a different study on the effects of livestock grazing (Krannitz 2008). After visiting each potential site, only nine were suitable for use in the southern Okanagan and I added one site from Washington State adjacent to the border (Fig. 1). Grazing history was not associated with ponderosa pine density at the sites (r_s = 0.08, $P = 0.83$, $n = 10$) (Krannitz and Rohner 2000) and, hence, was not a confounding factor on influence of tree density on the bird assemblage. The sites had varying densities of trees (Table 1), but this did not affect their biophysical classification (AN), or the biogeoclimatic zone and subzone under which they were also classified: BGxh1 (Bunchgrass, very dry hot [Nicholson et al. 1991]).

The sites were rectangular, 250 × 400–1,000 m, ranging in size from 10 to 25 ha (Table 1). Smaller sites did not have fewer species of breeding birds ($r_s = 0.34$, $P > 0.20$, $n = 10$), probably because sites were generally not fragments and were surrounded by similar habitat.

Surveys.—I used spot mapping to estimate bird abundance at each site (Bibby et al. 1992). Birds at each site in May 1994 and 1995 were mapped six times each year with visits spread as evenly as possible from 3 May to 1 June in 1994 and 1 May to 7 June in 1995 (117 visits). All birds encountered were noted on a map that corresponded to a 50 × 50 m grid system marked with flags on site. Individual birds were conservatively mapped to avoid double-counts of the same individual and a special effort was made to record simultaneous encounters of different individuals. Visits ranged from 20 to 90 min per site.

Encounter rate was standardized per km^2 to account for differences in site size with an average effort (± SE) of 251 ± 15 min/km^2 per visit in 1994 and 239 ± 11 min/km^2 per visit in 1995. Most surveys were conducted in the morning with a few in the evening (85% of visits between 0500 and 0900 hrs). I balanced the time of visits among sites to avoid bias attributable to time of day.

Vegetation characteristics were measured in June 1995 by first dividing each site into 75-m segments (5–13 segments per site, Table 1). The number of ponderosa pine >2 m in height was counted in each segment. A 120-m line intercept was conducted in the center of each segment (i.e., at 37.5 m), perpendicular to the length of the transect, to estimate linear cover of antelope bitterbrush (Brower et al. 1989). I estimated cover of bunchgrass and bare soil in six randomly placed 20 × 50 cm Daubenmire (1959) plots within each segment along the 120-m line intercept. Only plot locations between shrubs were chosen because of previously identified differences in vegetation beneath shrub canopies versus shrub interspaces (Krannitz 2008). Daubenmire cover classes were used (1–5, >5–25, >25–50, >50–75, >75–95, >95–100%) with one for <1%. Averages of the segments in a site were used to describe site differences and percent values were arcsine square-root transformed to improve normality and homoscedasticity.

Encounter rate was used to estimate bird abundance and was the number of observations of a bird species/visit/km^2. An average of encounter rate between years was used to assess the relationship between encounter rate and ponderosa pine density. A number of factors made this possible. First, search effort per visit and unit area did not differ between years (Wilcoxon paired rank test, $Z_{52} = -0.77$, $P = 0.44$). Second, encounter rate of species at specific sites in 1995 could be predicted from observations in 1994 (regression through origin including sites with at least one observation in either year: $y = 0.93x$, $r^2 = 0.49$, $n = 351$, $P < 0.0001$). The amount of variation

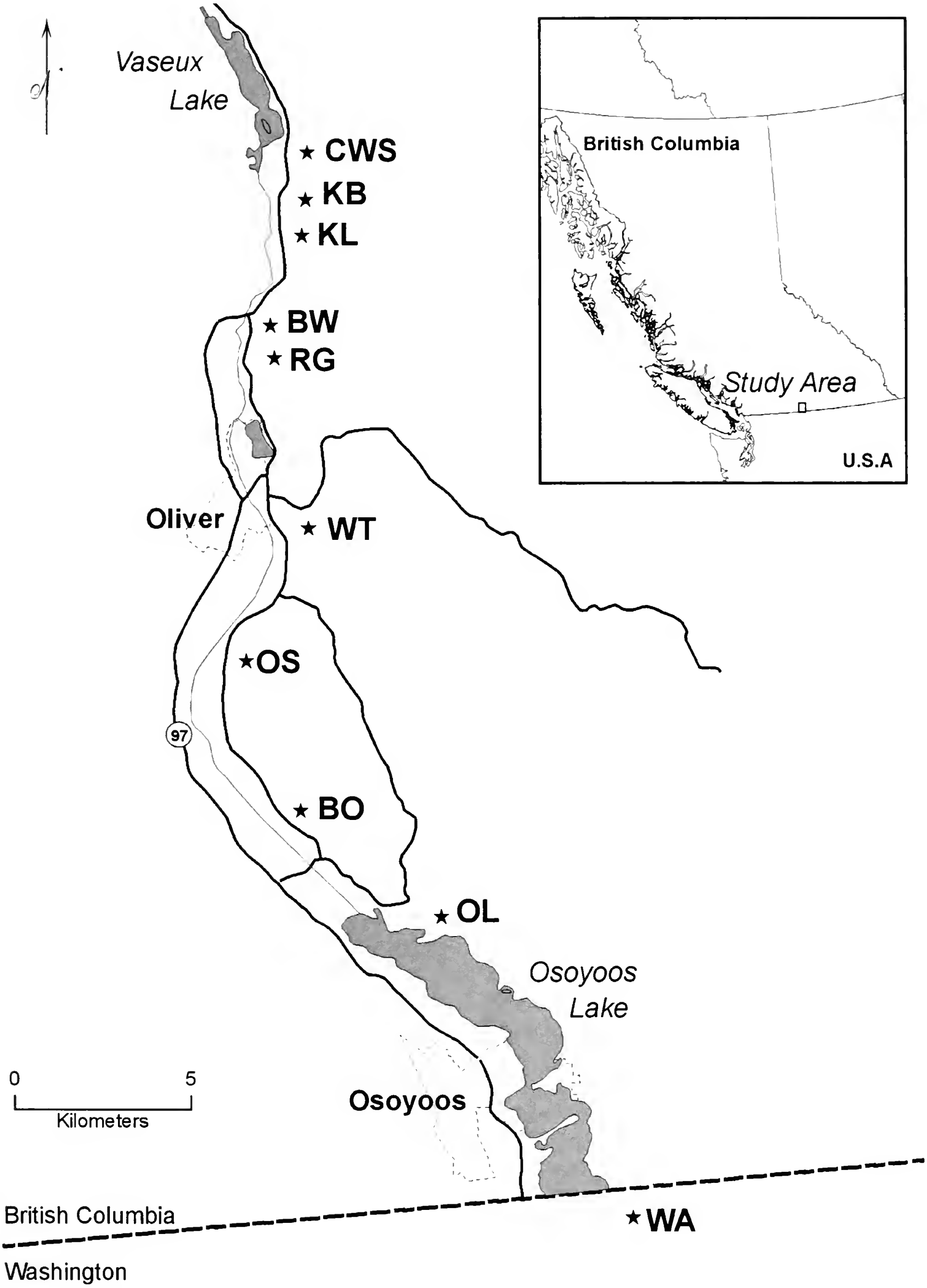

FIG. 1. Study sites (*) in the southern Okanagan Valley, British Columbia, Canada and northern Washington, United States.

explained was even higher (r^2 = 0.68) when only species with estimations of breeding density were included. Encounter rate was divided into four guilds following Ehrlich et al. (1988) (grassland/shrub-steppe, open woodland, closed canopy forest, and generalist) to examine if different groups of birds responded to trees differently.

TABLE 1. Characteristics of 10 study sites invaded by ponderosa pine in the southern Okanagan Valley, British Columbia, Canada in 1994–95. Averages (± SE) are derived from n values from the number of 75-m divisions within each 250-m wide site. AB = antelope bitterbrush.

Site	Pine density/ha	AB (% linear cover)	All shrubs (% cover)	Elev (m)	Size (ha)	n
BW	0.89 ± 0.60	22.87 ± 4.97	24.55 ± 0.60	336	12.5	6
KB	9.07 ± 2.85	24.19 ± 3.77	28.86 ± 2.74	452	12.5	6
WA	0	21.48 ± 2.93	24.05 ± 2.98	355	18.75	10
BO	0	31.32 ± 4.07	35.27 ± 3.83	352	18.75	10
CWS	22.61 ± 11.49	31.31 ± 1.36	33.79 ± 1.09	371	10	5
KL	9.15 ± 1.77	29.97 ± 3.08	31.30 ± 2.99	340	25	13
OS	27.06 ± 12.06	42.62 ± 2.82	48.7 ± 2.44	369	12.5	6
WT	1.42 ± 0.58	14.14 ± 2.56	16.52 ± 2.98	476	22.5	12
RG	1.51 ± 0.44	15.45 ± 2.60	21.45 ± 2.86	339	22.5	12
OL	0	8.16 ± 1.26	24.81 ± 2.15	356	25	12

Data Analysis.—The Shannon-Wiener Index of species diversity was calculated with program DIVERS (Krebs 1989). Correlation analysis was used to assess the association between total avian diversity and encounter rate of breeding birds with ponderosa pine density. Non-parametric Spearman Rank coefficients (r_s) were calculated (PROC CORR) (SAS Institute 1990) for all correlations.

I used canonical correspondence analysis (CCA) (Ter Braak and Šmilauer 1998) to identify the relative importance of ponderosa pine density versus other habitat variables on the bird assemblage, including transient birds such as migrants and visitors. Encounter rate of a bird species was included for those present at five or more of the sites. Habitat variables included were: arcsine square-root transformed percent cover of bare soil and bunchgrass, and linear cover of antelope bitterbrush, along with $\log_{10}(+1)$–transformed ponderosa pine density/ha, and elevation (m). A Monte Carlo randomization test was performed to test for significant effects (Ter Braak and Šmilauer 1998).

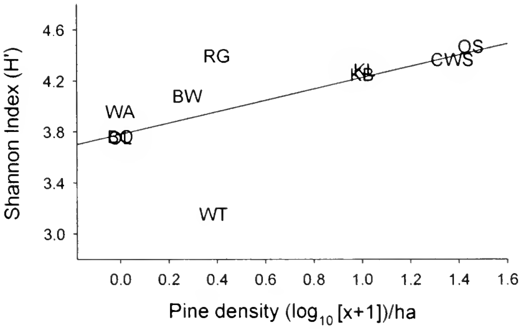

FIG. 2. Diversity of birds at 10 sites dominated by antelope bitterbrush with invading ponderosa pine in the southern Okanagan Valley, British Columbia, Canada.

RESULTS

There were 4,281 bird sightings during 117 visits at the 10 study sites. Eighty species of birds were observed (27–44 at individual sites, $\bar{x}$ [± SE] = 35.1 ± 1.4) (Appendix). Encounter rates ranged from 157.0 to 254.0 birds/km^2 ($\bar{x}$ = 215.0 ± 4.79).

Bird Diversity.—Thirty-eight species were breeding at the 10 sites; the other species were either transients or visitors from nearby habitats (20–29 at individual sites, $\bar{x}$ = 24.8 ± 0.74) (Appendix). Species diversity of breeding birds ranged from 2.73 to 4.17 (H′ average = 3.69 ± 0.13). Diversity was associated with $\log_{10}$-transformed ponderosa pine density ($r_s = 0.82$, $P < 0.01$ [H′]) (Fig. 2). The encounter rate of breeding birds was also associated with $\log_{10}$-transformed pine density ($r_s = 0.66$, $P = 0.04$).

Site WT (Table 1) was an outlier with comparatively low avian diversity of breeding birds (Fig. 2). This particular site was dominated by Vesper Sparrows (scientific names in Appendix). Almost 40% (166) of 424 observations of birds at this site in both 1994 and 1995 were of this species. Site OS (Table 1) with the highest diversity of breeding birds, had the same number of observations (426) and the same total number of species as WT. Diversity was higher at OS because observations of species were more evenly distributed. For example, the two most abundant birds,

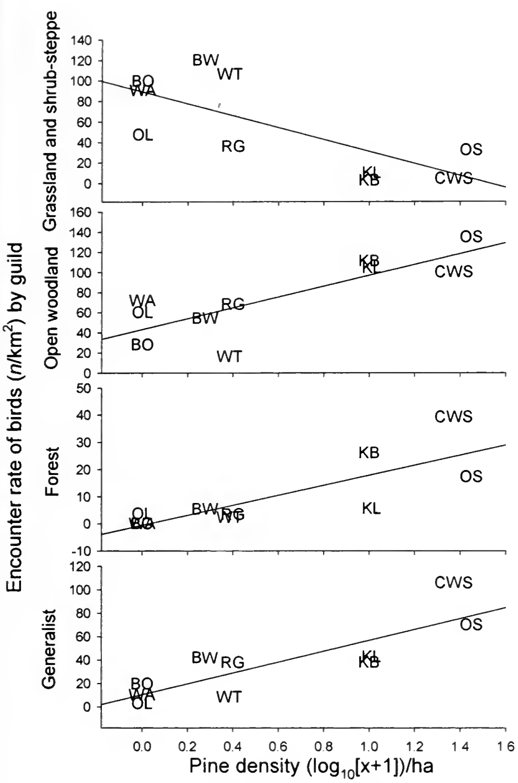

FIG. 3. Encounter rate of four habitat guilds (Appendix), averaged between years for each species and summed across species within a guild, in relation to average ponderosa pine density/ha at each site, southern Okanagan Valley, British Columbia, Canada.

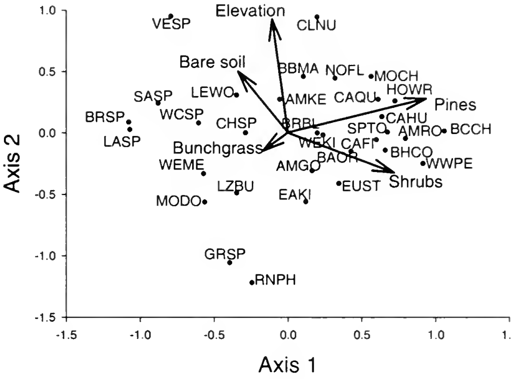

FIG. 4. Relationship of environmental factors (Axis 1) to encounter rate (Axis 2) of common breeding and transient birds (Appendix) in the southern Okanagan Valley, British Columbia, Canada.

Brown-headed Cowbird and Spotted Towhee were observed 53 and 51 times, respectively.

Different habitat guilds of birds responded differently to increasing ponderosa pine density. Breeding birds associated with grasslands and shrub-steppe were less abundant in more heavily forested sites ($r_s = -0.69$, $P = 0.026$, Fig. 3), while birds normally associated with open woodland ($r_s = 0.72$, $P = 0.02$) and forested ($r_s = 0.81$, $P = 0.005$) habitats became more abundant (Fig. 3). Species with generalist habitat preferences ($r_s = 0.83$, $P = 0.003$) and bird species known to prey on or parasitize nests of other birds ($r_s = 0.72$, $P = 0.019$) also increased in abundance with log-transformed ponderosa pine density.

The most common non-grassland or shrub-steppe birds, Brown-headed Cowbird and Spotted Towhee, were positively correlated with ponderosa pine density ($r_s = 0.755$, $P < 0.01$, and $r_s = 0.705$, $P < 0.05$ respectively, $n = 10$), whereas most grassland and shrub-steppe birds consistently showed a negative association with ponderosa pine density (Western Meadowlarks, $r_s = -0.706$, $P < 0.05$; Brewer's Sparrows, $r_s = -0.789$, $P < 0.01$; Lark Sparrows, $r_s = -0.831$, $P < 0.01$; Grasshopper Sparrows, $r_s = -0.805$, $P < 0.01$). Vesper Sparrows were the exception and were not more abundant on treeless sites ($r_s = -0.449$, $P > 0.1$).

Ponderosa pine density was most strongly associated with distribution of birds among the 10 sites (Fig. 4, Table 2). Elevation was

TABLE 2. Environmental factors and their strength in explaining the distribution of bird species among 10 antelope bitterbrush sites in southern Okanagan Valley of British Columbia, Canada.

Factor	Lambda	*F*	*P*
Density of ponderosa pine/ha	0.32	3.02	0.002
Elevation	0.16	1.63	0.078
Bunchgrass cover	0.14	1.42	0.182
Linear cover of antelope bitterbrush	0.11	1.23	0.272
Bare soil cover	0.07	0.73	0.618

marginally associated with distribution of birds (Fig. 4, Table 2), and this was independent of the effect of elevation on pine density (r_s = 0.28, P = 0.44, n = 10). Differences among sites in cover of bunchgrass, antelope bitterbrush, and bare soil did not affect the bird assemblage (Table 2). Cumulative percent variance of the species data explained by Axis 1 was 29.1 with Axis 2 explaining an additional 13.4%. Ponderosa pine density was associated with Axis 1 (r_p = 0.91) as was cover of antelope bitterbrush (r_p = 0.66), but they were not correlated with each other (r_s = 0.53, P = 0.11, n = 10). Axis 2 was associated with elevation (r_p = 0.89) and cover of bare soil (0.51), which were also not correlated with each other (r_s = 0.41, P = 0.24, n = 10). None of the other habitat variables was correlated with each other except for a marginally negative association between bare soil and linear cover of antelope bitterbrush (r_s = −0.60, P = 0.067, n = 10).

Birds associated with sites with more pines included House Wren, Black-capped and Mountain chickadees, Calliope Hummingbird, and Spotted Towhee (Fig. 4). Not surprisingly, grassland and shrub-steppe birds such as Western Meadowlark, Lark Sparrow, Brewer's Sparrow, and Vesper Sparrow were positioned away from ponderosa pine, as was the most abundant species observed during migration, White-crowned Sparrow (Fig. 4).

DISCUSSION

Bird diversity in the southern Okanagan Valley in British Columbia, Canada was comparable with other grassland and shrub-steppe studies in the Intermountain West. In the Chilcotin grasslands, Hooper and Pitt (1996) found 99 species at 13 study sites with a density of 109–165 pairs/km², similar to 114–255 pairs/km² found in this study. In the shrub-steppe of eastern Washington, Dobler et al. (1996) recorded 93 species over 3 years at 55 sites and in Oregon, densities of birds ranged from 100 to 600 individuals/km² (Wiens and Rotenberry 1981). My sites were dominated by antelope bitterbrush, rather than sagebrush (*Artemisia tridentata*) which is the more common shrub-steppe dominant species (West 1983, 1988). Sagebrush habitats in the southern Okanagan and Similkameen valleys have a similar number of bird species (98 species over 245 point count stations) (Paczek 2002).

The sites varied in cover of antelope bitterbrush, bare soil, and perennial bunchgrass but these characteristics were not important in affecting composition of the bird assemblage, compared to density of encroaching ponderosa pine. Not only were grassland and shrub-steppe birds less abundant at sites with more pines, but generalist bird species including nest predators such as corvids were more abundant. Corvids are known to prey on nests of shrub-steppe birds (Vander Haegen et al. 2002) and may use perches such as trees at edges (Söderström et al. 1998). Thus, trees invading grassland areas could have deleterious effects on grassland and shrub-steppe birds.

Coniferous trees have been increasing in density and invading grassland and shrub-steppe areas throughout western North America (Mast et al. 1997, Bai et al. 2004). This includes the southern Okanagan Valley, where burned sites had fewer trees than were present in 1938, and unburned sites had more trees (Turner and Krannitz 2001). In addition, climate change is resulting in pine invasion; periods of ponderosa pine establishment have been linked to increased spring moisture and reduced fire frequency associated with El Niño events (Brown and Wu 2005, League and Veblen 2006). Grassland and shrub-steppe birds (such as Brewer's Sparrow; Welstead 2002) may minimize the negative effect of tree invasion by choosing nest sites away from trees. However, if tree densities continue to increase, there will be increasingly less suitable habitat adjacent to the forest ecotone. Restoration efforts are underway to decrease tree densities and reintroduce fire in a controlled manner throughout the range of ponderosa pine (Covington et al.1997, Monleon et al. 1997, Thies et al. 2005).

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APPENDIX. Bird species observed on study sites with AOU code, observations summed over 1994 and 1995, nest predator or parasite (yes [Y] or no [N], from Cannings et al. 1987), habitat guild (Grassland/shrubsteppe [GR], Open forest [O], Forest [F], Generalist [G] from Ehrlich et al. 1988), and status (potentially breeding [B] or transients [migrants and visitors] [T]). Migrants and visitors from other habitats outside of study sites were not classified to habitat guild or included as potential nest predators.

AOU code	Common name	Scientific name	Obs	Nest pred. or par.?	Guild	Status
AMCR	American Crow	*Corvus brachyrhynchos*	9	Y	G	T
AMGO	American Goldfinch	*Carduelis tristis*	124	N	O	B
AMKE	American Kestrel	*Falco sparverius*	10			T
AMRO	American Robin	*Turdus migratorius*	130	N	G	B
BBMA	Black-billed Magpie	*Pica hudsonia*	226	Y	O	B
BCCH	Black-capped Chickadee	*Poecile atricapillus*	19	N	F	B
BCHU	Black-chinned Hummingbird	*Archilochus alexandri*	1			T
BHCO	Brown-headed Cowbird	*Molothrus ater*	206	Y	G	B
BLJA	Blue Jay	*Cyanocitta cristata*	1			T
BRBL	Brewer's Blackbird	*Euphagus cyanocephalus*	32	N	G	B
BRSP	Brewer's Sparrow	*Spizella breweri*	107	N	GR	B

APPENDIX. Continued.

AOU code	Common name	Scientific name	Obs	Nest pred. or par.?	Guild	Status
BUOW	Burrowing Owl	*Athene cunicularia*	3	N	GR	B
CAFI	Cassin's Finch	*Carpodacus cassinii*	103	N	O	B
CAHU	Calliope Hummingbird	*Stellula calliope*	90	N	O	B
CAQU	California Quail	*Callipepla californica*	195	N	G	B
CAWR	Canyon Wren	*Catherpes mexicanus*	11			T
CCSP	Clay-colored Sparrow	*Spizella pallida*	10			T
CHSP	Chipping Sparrow	*S. passerina*	165	N	O	B
CHUK	Chukar	*Alectoris chukar*	11	N	GR	B
CLNU	Clark's Nutcracker	*Nucifraga columbiana*	24	N	F	B
COHA	Cooper's Hawk	*Accipiter cooperi*	1			T
CONI	Common Nighthawk	*Chordeiles minor*	1			T
CORA	Common Raven	*Corvus corax*	8	Y	G	B
DOWO	Downy Woodpecker	*Picoides pubescens*	3			T
DUFL	Dusky Flycatcher	*Empidonax oberholseri*	2			T
EAKI	Eastern Kingbird	*Tyrannus tyrannus*	14			T
EUST	European Starling	*Sturnus vulgaris*	77	Y	G	B
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	6			T
GCSP	Golden-crowned Sparrow	*Zonotrichia atricapilla*	10			T
GRCA	Gray Catbird	*Dumetella carolinensis*	3			T
GRPA	Gray Partridge	*Perdix perdix*	2			T
GRSP	Grasshopper Sparrow	*Ammodramus savannarum*	18	N	GR	B
HAWO	Hairy Woodpecker	*Picoides villosus*	1			T
HOFI	House Finch	*Carpodacus mexicanus*	9			T
HOWR	House Wren	*Troglodytes aedon*	23	N	O	B
KILL	Killdeer	*Charadrius vociferus*	16			T
LASP	Lark Sparrow	*Chondestes grammacus*	56	N	GR	B
LBCU	Long-billed Curlew	*Numenius americanus*	2			T
LEWO	Lewis's Woodpecker	*Melanerpes lewis*	36	N	O	B
LZBU	Lazuli Bunting	*Passerina amoena*	43	N	O	B
MOBL	Mountain Bluebird	*Sialia currucoides*	2			T
MOCH	Mountain Chickadee	*Poecile gambeli*	30	N	F	B
MODO	Mourning Dove	*Zenaida macroura*	178	N	GR	B
NAWA	Nashville Warbler	*Vermivora ruficapilla*	11	N	F	B
NOFL	Northern Flicker	*Colaptes auratus*	81	N	O	B
NOHA	Northern Harrier	*Circus cyaneus*	2			T
BAUR	Baltimore Oriole	*Icterus galbula*	159	N	O	B
OCWA	Orange-crowned Warbler	*Vermivora celata*	2			T
PISI	Pine Siskin	*Carduelis pinus*	39			T
PUFI	Purple Finch	*Carpodacus purpureus*	13			T
PYNU	Pygmy Nuthatch	*Sitta pygmaea*	26	N	F	B
RBNH	Red-breasted Nuthatch	*S. canadensis*	1			T
RECR	Red Crossbill	*Loxia curvirostra*	29			T
RNPH	Ring-necked Pheasant	*Phasianus colchicus*	49	N	GR	B
ROPI	Rock Pigeon	*Columbia livia*	69			T
ROWR	Rock Wren	*Salpinctes obsoletus*	2			T
RTHA	Red-tailed Hawk	*Buteo jamaicensis*	1			T
RUBL	Rusty Blackbird	*Euphagus carolinus*	2			T
RUHU	Rufous Hummingbird	*Selasphorus rufus*	29	N	F	B
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	32			T
SAPH	Say's Phoebe	*Sayornis saya*	16	N	O	B
SASP	Savannah Sparrow	*Passerculus sandwichensis*	22			T
SOSP	Song Sparrow	*Melospiza melodia*	1			T
BHVI	Blue-headed Vireo	*Vireo solitarius*	2			T
SPTO	Spotted Towhee	*Pipilo maculatus*	216	N	O	B
STJA	Steller's Jay	*Cyanocitta stelleri*	3			T
TOSO	Townsend's Solitaire	*Myadestes townsendi*	1			T

APPENDIX. Continued.

AOU code	Common name	Scientific name	Obs	Nest pred. or par.?	Guild	Status
VESP	Vesper Sparrow	*Pooecetes gramineus*	265	N	GR	B
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	434			T
WEBL	Western Bluebird	*Sialia mexicana*	19	N	O	B
WEKI	Western Kingbird	*Tyrannus verticalis*	147	N	O	B
WEME	Western Meadowlark	*Sturnella neglecta*	517	N	GR	B
WETA	Western Tanager	*Piranga ludoviciana*	2			T
WIWA	Wilson's Warbler	*Wilsonia pusilla*	3			T
WIWR	Winter Wren	*Troglodytes troglodytes*	9	N	F	B
WWPE	Western Wood-pewee	*Contopus sordidulus*	15			T
YBCH	Yellow-breasted Chat	*Icteria virens*	1			T
YHBL	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	31			T
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	13	N	F	B
YEWA	Yellow Warbler	*D. petechia*	1			T

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SPRING ARRIVAL DATES OF MIGRATORY BREEDING BIRDS IN MAINE: SENSITIVITY TO CLIMATE CHANGE

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ABSTRACT.—I analyzed the relationship between spring temperature and arrival date for 105 species using over 32,000 arrival records of migratory breeding birds in Maine collected by a volunteer network between 1994 and 2005. I used quantile regression analysis, testing three different quantiles (0.1, 0.25, 0.5). Only 69 of 315 regressions yielded a significant negative relationship. Five species showed significant regressions for all three quantiles and 15 showed significant regressions for two quantiles. Quantile regressions of arrival date with a hemispheric measure of climate variability, the North Atlantic Oscillation index, produced only 63 statistically significant regressions for the three quantiles. Seven species and 12 species had significant regressions with three and two quantiles, respectively. Overall, 60 species had at least one significant relationship with a climatic variable. These results indicate the arrival dates of most migratory breeding birds in Maine show a modest relationship with the significant temperature variability seen over the 12-year study period. The data suggest the response of migratory birds in Maine to global warming impacts will be a gradual process. *Received 10 April 2006. Accepted 31 January 2007.*

The monotonic rise of atmospheric carbon dioxide over the past 150 years is certain evidence of global warming (Root et al. 2005, Smith et al. 2005). Melting of the polar ice caps and increased mean annual temperatures across the globe are but two manifestations of recent climate change attributed to the unprecedented rate of increase of greenhouse gases. Climate has a fundamental effect on the distribution and abundance of virtually all species. The northern extension of species such as American Robin (*Turdus migratorius*) in northern Alaska (Sallabanks and James 1999) or lepidopterans in Great Britain (Hill et al. 1999) has been linked to environmental warming. Species can adapt evolutionarily to global climate change, but the pace at which climate change appears to be occurring greatly concerns conservation biologists and resource managers.

Ecologists are concerned with the effects of global climate change on the population dynamics of species, but the effort and time required to assess those effects present daunting challenges (Crick 2004). To date, most of the impacts of global warming on organisms have been based on easier-to-measure phenological effects such as first flowering date or arrival dates for migratory animals (Sparks et al. 2001, Sparks and Menzel 2002).

Modeling is another approach to assess the impacts of global climate change. Modeling effects of climate change on vascular plants is reasonably straightforward because local temperature and precipitation serve as the main parameters in the models (e.g., Iverson et al. 1999). For example, models of the distribution of tree species in northeastern North America, assuming that carbon dioxide levels will continue to rise at current rates, indicate dramatic changes in distribution over the next 100 years (Iverson et al. 1999). Balsam fir (*Abies balsamea*), a dominant tree in northern New England is predicted to be extirpated by 2100. Changes in distribution and abundance of trees will have strong cascading effects on the animals that depend on particular tree species (e.g., Matthews et al. 2004).

Modeling the impact of global climate change for species that are migratory is much more complex (Cotton 2003, Sæther et al. 2004). Changes in temperature in wintering areas may impel earlier departures to northern breeding sites (Anthes 2004, Saino et al. 2004, Gordo et al. 2005). Temperature along the migratory route may influence timing of the continuation of migration. Finally, temperatures in breeding areas may affect the optimal time for nesting and reproductive success. Although migratory birds will be strongly affected by temperatures in their breeding areas, birds cannot predict the particular climate from afar (Lehikoinen et al. 2004). The appropriate temperature data to test as determinants of phenological events are not clear.

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Recent research has suggested that broad-scale climatic approaches to understanding the phenology of migration can be more informative than research based on local climate. A number of studies in western Europe and eastern North America have demonstrated that intensity of the North Atlantic Oscillation (NAO) strongly influences avian phenological events in Europe and North America (Huppop and Huppop 2003, Hubálek 2004, Vähätalo et al. 2004, Marra et al. 2005). The NAO is measured as the difference in pressure between the subtropical high centered over Portugal and the subarctic low centered over Iceland. Strong differences in pressure produce wet and warm winters in Europe and cold, dry winters in Canada and the northeastern United States. Reduced differences in pressure lead to colder winters in northern Europe and warmer, snowier winters in northeastern North America.

Birds are often touted as sensitive sentinels of environmental change. The detection of effects of global warming by measuring the demography of woody plants will be straightforward but may require decades to see definitive evidence. As mobile organisms with high metabolic demands, birds should be capable of responding more quickly to the direct effects of global warming on their own physiology and to the indirect effects of resource alteration (seed abundance, insect herbivore abundance). In this paper, I ask if migratory breeding birds in Maine respond in spring arrival dates to yearly differences in temperature using data from 1994 through 2005. I also examine the power of the NAO in affecting the arrival date of migratory breeding birds. My goal was not to seek evidence of earlier arrival dates over this brief 12-year period but rather to ask how sensitive arrival date is to temperature that varied significantly among the 12 years of the study.

METHODS

Data on arrival dates of migratory breeding birds in Maine come from a citizen-science project I organized in spring 1994 to improve our understanding of spring bird migration in Maine. This on-going project has now yielded data on arrival dates for the past 12 springs. The framework for data collection is the map of Maine biophysical regions developed by McMahon (1990) who divided the state into 15 biophysical regions based on climatic and vegetation data (Fig. 1). The south coastal region (Region 12) has the mildest climate with a frost-free period of 160 days compared to the most severe climate in the Boundary Plateau (Region 1) with a frost-free period of only 80 days (McMahon 1990).

Volunteer observers are sent a standardized data sheet and asked to report the first date of each migratory species they observe in their biophysical region. Some active birders regularly report arrival dates of a given species from several biophysical regions. The data sheet lists 119 species, all of which nest in at least one biophysical region in the state. Over 200 birders have contributed data to the project and the data base currently has over 32,000 arrival records. I report data on 105 species in this paper; data on the remaining 14 species were too sparse for meaningful statistical analysis.

The arrival dates of each record were converted to Julian day. For example, 31 March is the 100th day of the year (101st during leap years). Data for biophysical region of the observation, year, and Julian date were entered into a Stata data set for analysis.

Wilson et al. (1997) found that arrival dates of the vast majority of Maine migratory breeding birds for 1994–1997 did not vary across biophysical regions. The few differences that emerged were between the six northernmost zones and some southern zones. I excluded data from the six most northern zones (zones 1–6). Therefore, the data used for this paper were for only biophysical regions 7–15. Observations reflect the distribution of the human population in the state. The relatively populous regions 10, 12, and 13 accounted for 69.6% of the observations.

Both local temperature and hemispheric temperature data were used in the analysis. Data from the National Climatic Data Center (NCDC) were used as measures of local springtime temperatures. Rather than use daily or weekly temperature records, I chose to use monthly data as reasonable measurements of deviations from the average temperature (Table 1). I chose 11 stations across the study area that had complete data for the 12-year period. These stations were Farmington and Dover-Foxcroft in Region 7, Augusta, Lew-

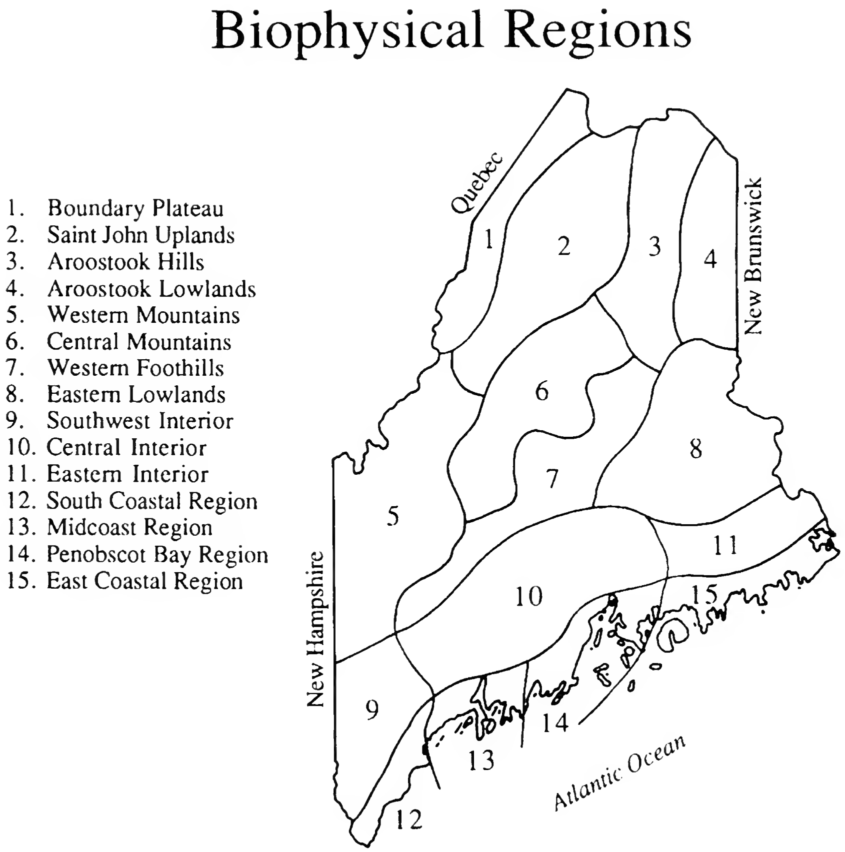

FIG. 1. Biophysical regions of Maine based on climatic and vegetative data (after McMahon 1990).

TABLE 1. Deviations from annual monthly temperature in °C of selected southern and central Maine weather stations as well as the North Atlantic Oscillation index, measured as the difference between the Icelandic subarctic low and the southwestern Europe subtropical high from December through March, 1994–2005.

Year	Mar	Apr	May	NAO Index
1994	−1.1	0.1	−0.7	3.03
1995	0.7	−1.3	−0.5	3.96
1996	−1.3	−0.1	−1.0	−3.78
1997	−1.8	−1.1	−1.9	−0.20
1998	1.4	1.2	2.5	0.72
1999	1.7	1.2	1.8	1.70
2000	2.7	0.1	−0.7	2.80
2001	−1.4	−0.3	1.4	−1.89
2002	0.3	0.5	−1.1	0.76
2003	−1.3	−1.3	−1.0	0.20
2004	0.8	0.3	0.3	−0.07
2005	−1.7	1.0	−2.6	0.12

iston, Madison, Orono, and Waterville in Region 10, Sanford in Region 12, Portland in Region 13, Belfast in Region 14, and Eastport in Region 15. Deviations from the monthly mean for each station were averaged for each year. Deviation data for combined March and April as well as April and May were prepared by averaging the means for each month.

I examined the relationship between Maine spring temperatures and temperatures in other states in the northeast and mid-Atlantic region by obtaining NCDC data on monthly deviation from the mean temperature for New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, New York, New Jersey, Pennsylvania, Delaware, and Maryland. The NCDC partitions most states into several divisions, each of which was considered separately. I used Pearson product-moment correlations to assess the relationship between the Maine temperature over the 12-year period with each division of the 10 other states for March, April, and May. I used the North Atlantic Oscillation winter index (Dec through Mar) as a measure of hemispheric weather. Values were obtained at: http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html.

I performed quantile regression analysis (Koenker and Hallock 2001, Cade and Noon 2003) using Stata (Macintosh) to examine if arrival dates were earlier in warmer springs for each of the 105 species of birds. This technique has an advantage over least-squares regression because quantile regression can accommodate unequal variation in the distribution of data. If such variation exists, a single rate of change (measured by the slope) will be misleading because portions of the data may produce different slopes. It is possible, for instance, that the relationship between the earliest arrivals and temperature deviation may be different than the relationship between median arrivals and temperature deviation. *A priori*, I expected the earliest arrival dates or the median arrival dates might be more sensitive to temperature deviations or to the NAO index than later arrivals. Accordingly, I tested the 0.1, 0.25 and 0.5 (median) quantiles. I do not report the data for the 0.75 and 0.9 quantiles which were heavily biased toward later first arrivals. Each quantile regression analysis uses all of the data in the data set.

The temperature data used reflected time of arrival of a particular species (Table 2). For instance, March temperature departures were used for the Red-winged Blackbird (scientific names in Table 2) analysis because most arrival dates were in March. The March–April combined temperature data were used for species such as American Woodcock for which arrival records spanned the latter half of March and the first half of April.

I performed analogous quantile regression analyses for the North Atlantic Oscillation data, regressing the NAO index against the same three quantiles of arrival for each of the 105 species in this study. When performing a large number of regressions, rejecting the null hypothesis of no relationship for each individual regression analysis at the $P = 0.05$ level may result in an erroneously high number of significant relationships (Davis 1989, Töttrup et al. 2006). I used the Bonferroni sequential procedure to produce a table-wide significance level of $P = 0.05$ to avoid this bias.

RESULTS

Temperatures for March, April, and May of each year of the study varied (Table 1). Examination of the deviation from the monthly mean for any given year indicates that some springs were consistently warmer (e.g., 1998) or cooler (e.g., 1997) for all 3 months. Some years had a mixed pattern with some months cooler than normal and others warmer than normal (e.g., 1995 and 2002). The magnitude of the departures from the mean indicate considerable variation among years (e.g., March 1997 vs. March 2000). The annual NAO Index for the 12 years of the study also varied among years (Table 1). Linear regressions of NAO against temperature deviation were not significant for any of the 3 months.

Correlation analysis of the Maine monthly temperature deviation data with corresponding data from other northeastern and mid-Atlantic States revealed a strong regional climatic signature. Deviations from the monthly mean for all New England states and New York were strongly correlated ($P < 0.01$) in every case for the March, April, and May data. About half of the correlations for Pennsylvania and New Jersey were statistically significant with even less concordance with temperature deviations for Delaware and Maryland. The data clearly indicate that New York and the six New England states have highly similar spring weather from year-to-year over the study period.

Temperatures and the total number of arrival dates reported by species varied (Table 2) across all years for Biophysical Regions 7–15. Median arrival dates over all years as well as the range of annual medians as a simple measure of variability among year also varied (Table 2).

The results of each of the quantile regressions, listing the value of the slope of the regression as a measure of the strength of the relationship, were not constant (Table 2). The most obvious result of the statistical analyses of the Maine temperature data was the absence of a significant regression between temperature and arrival date for most species and quantile combinations. Only 69 (21.9%) of the 315 regressions were statistically significant

TABLE 2. Species included in the analysis arranged in phylogenetic order. Number of arrival dates, grand mean of arrival date over the 12 years of the study, and the range of the 12 annual median dates for each species as an indication of variability are given. The temperature data used in the regression analysis are given. The slopes of the quantile regressions for temperature deviation and NAO index are provided. Statistically significant regressions are indicated by * ($0.01 < P \leq 0.05$) or ** ($P < 0.01$).

Species	*n*	Median arrival	Range of medians	Temp range	Temp departure			NAO index		
					0.1	0.25	0.5	0.1	0.25	0.5
Wood Duck (*Aix sponsa*)	253	4/7	17	Mar/Apr	−1.66	−0.23	−0.60	−0.16	−0.57	−0.59
Green-winged Teal (*Anas crecca*)	199	4/21	17	Apr	−2.19	0.02	−0.94	−1.27	−1.02	−1.79**
Blue-winged Teal (*A. discors*)	134	4/4	24	Mar/Apr	−0.87	0.19	−0.53	−0.24	−1.04	−0.21
Ring-necked Duck (*Aythya collaris*)	246	3/29	20	Mar/Apr	−2.01	−0.34	−1.14	−0.37*	−0.61	−0.95
Common Loon (inland only) (*Gavia immer*)	148	4/16	13	Apr	−0.76	−1.33*	−0.67	−1.05	−0.74	−0.34
Pied-billed Grebe (*Podilymbus podiceps*)	99	4/15	20	Apr	−1.09	−1.22	−1.76	−1.29	−0.97	−0.47
American Bittern (*Botaurus lentiginosus*)	165	4/30	17	Apr/May	1.17	1.88	1.40	−0.77	−1.50**	−1.57*
Great Blue Heron (*Ardea herodias*)	415	4/9	12	Mar/Apr	1.35*	0.52	−0.39	−0.72	−0.76**	−1.76**
Green Heron (*Butorides virescens*)	112	5/6	17	Apr/May	3.74	1.38	0.25	0.42	1.10	−0.11
Black-crowned Night-heron (*Nycticorax nycticorax*)	84	5/5	19	Apr/May	2.69	1.45	1.32	−0.40	1.27	1.93
Glossy Ibis (*Plegadis falcinellus*)	92	4/16	35	Apr	0.99	−0.09	0.50	−0.48	0.30	−0.22
Turkey Vulture (*Cathartes aura*)	424	4/8	35	Mar/Apr	−1.21	−1.12	−1.08	−1.10*	−0.52	−0.68
Osprey (*Pandion haliaetus*)	382	4/15	11	Apr	−0.49	−0.76	−0.50	−0.99**	−0.77*	−0.53
Northern Harrier (*Circus cyaneus*)	304	4/12	43	Apr	−0.27	0.98	−0.01	−0.98	−1.06*	−0.76
Broad-winged Hawk (*Buteo platypterus*)	312	4/26	7	Apr	−0.34	−0.48	0.38	−0.61	−0.27	0.28
American Kestrel (*Falco sparverius*)	398	4/3	18	Mar/Apr	−0.19	0.86	−0.31	−1.40**	−1.18**	−1.78**
Virginia Rail (*Rallus limicola*)	96	5/9	13	May	0.96	−0.17	−0.42	−2.33	−0.75	0.07
Sora (*Porzana carolina*)	93	5/12	14	May	0.18	0.28	−0.00	−0.11	0.29	1.06
Killdeer (*Charadrius vociferus*)	405	3/28	14	Mar/Apr	−2.03*	−1.48**	−0.43	−0.52	−1.48**	−0.43
Willet (*Catoptrophorus semipalmatus*)	82	5/8	13	May	−2.29	0.31	−0.74	0.15	−0.17	0.11
Upland Sandpiper (*Bartramia longicauda*)	74	5/12	21	May	0.43	0.18	0.22	0.34	0.37	−1.06*
Spotted Sandpiper (*Actitis macularia*)	190	5/14	11	May	−0.50	−0.13	−0.11	−0.36	−0.22	−0.11
Wilson's Snipe (*Gallinago delicata*)	191	5/19	13	Apr	−0.91	−1.22*	−0.73	−0.25	−0.61	−1.20**
American Woodcock (*Scolopax minor*)	312	3/29	16	Mar/Apr	−3.08**	−1.34**	−0.89**	0.20	−0.53	−0.82**

TABLE 2. Continued.

Species	*n*	Median arrival	Range of medians	Temp range	Temp departure			NAO index		
					0.1	0.25	0.5	0.1	0.25	0.5
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	82	5/27	13	May	−3.31	−0.42	−0.79*	1.02	0.15	0.01
Common Nighthawk (*Chordeiles minor*)	131	5/26	16	May	−0.20	−0.26	−0.63	−0.59	0.14	−0.27
Whip-poor-will (*Caprimulgus vociferus*)	66	5/19	14	May	0.09	−0.22	−0.46	−0.73	0.14	−0.10
Chimney Swift (*Chaetura pelagica*)	251	5/11	9	May	−0.07	−0.16	−0.11	−0.26	−0.14	−0.45*
Ruby-throated Hummingbird (*Archilochus colubris*)	438	5/10	8	May	0.02	−0.26	−0.36**	0.83**	0.16	0.37
Belted Kingfisher (*Ceryle alcyon*)	367	4/19	13	Apr	1.74	0.59	−0.52	−2.47**	−2.21**	−1.01**
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	236	4/19	10	Apr	−1.27	−2.05**	−1.14**	−0.47	−0.45	−0.24
Northern Flicker (*Colaptes auratus*)	464	4/14	15	Apr	0.38	−0.59	−1.41**	−0.36	−1.60**	−1.31**
Olive-sided Flycatcher (*Contopus cooperi*)	101	5/25	9	May	−2.48	−1.03**	−0.42	−0.11	−0.21	−0.09
Eastern Wood-pewee (*C. virens*)	233	5/24	6	May	−0.45	−0.53	−0.67**	−0.26	0.19	0.16
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	90	5/23	11	May	−2.36	−0.59*	−0.33	1.95	−0.12	0.00
Alder Flycatcher (*E. alnorum*)	157	5/25	11	May	0.71	0.36*	−0.20	−0.73	−0.34	−0.01
Willow Flycatcher (*E. trailii*)	79	5/26	6	May	0.23	0.00	−.30	0.11	0.00	0.42
Least Flycatcher (*E. minimus*)	242	5/13	13	May	−0.91**	−0.65**	−0.47	0.54	0.04	0.16
Eastern Phoebe (*Sayornis phoebe*)	467	4/7	21	Mar/Apr	−0.07	−0.28	−0.26	−0.68**	−1.06**	−1.71**
Great Crested Flycatcher (*Myiarchus crinitus*)	301	4/30	8	Apr/May	−0.32	−0.78**	−0.83	0.36	0.07	0.13
Eastern Kingbird (*Tyrannus tyrannus*)	377	5/14	10	May	−0.19	−0.38	−0.20	−0.15	−0.13	−0.12
Blue-headed Vireo (*Vireo solitarius*)	331	5/2	14	Apr/May	−0.62	−0.65	−0.66**	−0.26	−0.05	−0.03
Warbling Vireo (*V. gilvus*)	183	5/14	13	May	−1.13**	−0.51**	−0.74*	−0.21	−0.42*	−0.29
Red-eyed Vireo (*V. olivaceus*)	302	5/16	8	May	−0.62	−0.95**	−0.47*	−0.45	−0.16	0.05
Tree Swallow (*Tachycineta bicolor*)	497	4/13	13	Apr	−0.52	−0.30	−0.27	−0.74**	−0.98**	−1.20**
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	148	5/5	16	Apr/May	1.38	−0.13	−0.32	0.23	0.46	0.57
Bank Swallow (*Riparia riparia*)	136	5/17	9	May	1.75	−0.38	0.05	0.44	−0.30	−0.56
Cliff Swallow (*Petrochelidon pyrrhonota*)	157	5/14	13	May	0.08	0.35	0.12	−0.58	−1.11	−0.16
Barn Swallow (*Hirundo rustica*)	364	5/5	8	Apr/May	−0.65	−0.64	0.11	−0.98*	−0.24	0.21
House Wren (*Troglodytes aedon*)	156	5/9	12	May	−0.13	−0.69*	−1.23**	0.29	0.29	−0.03

TABLE 2. Continued.

Species	*n*	Median arrival	Range of medians	Temp range	Temp departure			NAO index		
					0.1	0.25	0.5	0.1	0.25	0.5
Winter Wren (*T. troglodytes*)	191	4/19	21	Apr	−1.78	−1.48	−1.79**	0.07	−1.10*	−0.89*
Marsh Wren (*Cistothorus palustris*)	80	5/17	7	May	0.91	−0.42	−0.91	0.52	1.71**	0.88
Ruby-crowned Kinglet (*Regulus calendula*)	302	4/21	25	Apr	−1.52**	−1.02**	−1.28**	−0.80**	−1.01**	−1.28**
Blue-gray Gnatcatcher (*Polioptila caerulea*)	92	5/8	16	Apr/May	2.63	1.67	0.96	−0.82	−0.93	−0.26
Eastern Bluebird (*Sialia sialis*)	308	4/7	15	Mar/Apr	−1.65	−0.81	−1.51	−0.23	−0.57	−1.70
Veery (*Catharus fuscescens*)	304	5/16	7	May	−0.30	−0.25	−0.16	−0.09	−0.01	0.14
Swainson's Thrush (*C. ustulatus*)	156	5/18	9	May	−1.81	−1.00**	−0.51	0.30	−0.09	0.07
Hermit Thrush (*C. guttatus*)	374	4/22	13	Apr	−1.70**	−0.56**	0.04	−0.99**	−0.83**	0.04
Wood Thrush (*Hylocichla mustelina*)	293	5/12	8	May	−0.12	−0.11	−0.28	−0.25	−0.29	−0.29
American Robin (*Turdus migratorius*)	413	3/21	7	Mar	0.00	−0.90	−0.69**	0.00	0.25	−0.43
Gray Catbird (*Dumetella carolinensis*)	420	5/11	12	May	−0.16	−0.21	−0.25	−0.01	0.07	−0.18
Brown Thrasher (*Toxostoma rufum*)	209	5/8	12	May	−0.03	−0.19	−0.21	−0.44	−0.66	0.07
Tennessee Warbler (*Vermivora peregrina*)	118	5/20	17	May	−0.76	0.05	−0.47*	−0.36	−0.29	−0.11
Nashville Warbler (*V. ruficapilla*)	298	5/10	8	May	0.33**	−0.30	−0.33*	−0.22	0.03	−0.41**
Northern Parula (*Parula americana*)	380	5/9	9	May	−0.32**	−0.47**	−0.73**	−0.01	0.26	0.20
Yellow Warbler (*Dendroica petechia*)	404	5/12	8	May	−0.28	0.29	0.23	0.26	−0.29	−0.54
Chestnut-sided Warbler (*D. pensylvanica*)	358	5/12	11	May	−0.91**	−0.28*	−0.16	−0.57*	−0.47**	0.00
Magnolia Warbler (*D. magnolia*)	304	5/15	7	May	−0.55**	−0.39**	0.00	−0.73**	−0.56**	0.00
Cape May Warbler (*D. tigrina*)	100	5/15	11	May	−0.91**	−0.28*	−0.16	−0.56*	−0.47**	0.00
Black-throated Blue Warbler (*D. caerulescens*)	270	5/13	8	May	−0.38*	0.84	0.00	0.05	−0.57	0.00
Yellow-rumped Warbler (*D. coronata*)	439	4/28	12	May	0.18	0.42	−0.36	−0.42	0.03	0.20
Black-throated Green Warbler (*D. virens*)	406	5/8	16	May	−0.36**	−0.60**	−0.45	−0.12	0.10	0.00

TABLE 2. Continued.

Species	*n*	Median arrival	Range of medians	Temp range	Temp departure			NAO index		
					0.1	0.25	0.5	0.1	0.25	0.5
Blackburnian Warbler (*D. fusca*)	253	5/16	6	May	−0.46	−0.30	−0.39*	0.05	0.28	0.17
Pine Warbler (*D. pinus*)	263	4/20	9	Apr	−1.85**	−1.52**	−0.19	−0.96**	−0.84**	−0.50
Prairie Warbler (*D. discolor*)	93	5/12	17	May	−0.65	−0.15	−0.95	0.03	−0.44	−0.95
Palm Warbler (*D. palmarum*)	264	4/22	11	Apr	−0.74	−0.39	0.02	−1.03**	−0.72**	−0.27
Bay-breasted Warbler (*D. castanea*)	129	5/19	10	May	−0.25	0.00	−0.54	0.13	0.00	−0.32
Blackpoll Warbler (*D. striata*)	176	5/20	7	May	−0.14	−0.13	−0.43	0.07	−0.06	−0.29
Black-and-white Warbler (*Mniotilta varia*)	420	5/6	10	Apr/May	−0.12	−0.19	−0.19	−0.40	−0.28*	−0.42
American Redstart (*Setophaga ruticilla*)	353	5/15	6	May	−0.60**	−0.28*	0.00	−0.72**	−0.29	0.00
Ovenbird (*Seiurus aurocapillus*)	396	5/9	7	May	−0.50**	−0.07*	−0.50	0.04	0.22	0.15
Northern Waterthrush (*S. noveboracensis*)	219	5/9	12	May	0.09	−0.45	−0.79**	−0.44	−0.12	−0.43
Mourning Warbler (*Oporornis philadelphia*)	68	5/7	9	May	−0.44	0.24	0.44	1.03	0.44	0.56
Common Yellowthroat (*Geothlypis trichas*)	402	5/26	8	May	−0.05	−0.06	0.14	−0.29	−0.27	0.31
Wilson's Warbler (*Wilsonia pusilla*)	188	5/13	8	May	−0.39	−0.38**	−0.43	−0.14	0.04	0.00
Canada Warbler (*W. canadensis*)	215	5/16	5	May	0.00	0.00	0.00	0.00	0.00	0.00
Scarlet Tanager (*Piranga olivacea*)	265	5/20	7	May	−0.15	−0.12	−0.60	−0.22	0.29	−0.60**
Eastern Towhee (*Pipilio erythrophthalmus*)	208	5/19	19	Apr/May	−0.42	−0.74	−0.99*	0.12	0.48	1.20
Chipping Sparrow (*Spizella passerina*)	457	5/4	13	Apr	−0.25	−0.42	−0.61	0.62	−0.36	0.32
Field Sparrow (*S. pusilla*)	121	4/25	14	Apr/May	−0.21	−0.31	1.14	0.12	0.08	0.36
Vesper Sparrow (*Pooecetes gramineus*)	95	5/4	16	Apr/May	0.13	−0.23	0.55	−0.42	−1.10	−1.40
Savannah Sparrow (*Passerculus sandwichensis*)	290	3/28	10	Apr	1.52	0.17	0.36	−0.83	−0.75**	0.36
Fox Sparrow (*Passerella iliaca*)	217	5/1	20	Mar/Apr	−3.02**	−1.29**	−0.43	0.42	−0.61**	0.12
Song Sparrow (*Melospiza melodia*)	388	4/24	21	Mar/Apr	−0.95	−0.65	−0.09	−0.68	−0.89*	−1.02**
Lincoln's Sparrow (*M. lincolnii*)	116	5/14	16	May	−4.28	−3.82**	−0.88	2.43	1.59	0.44
Swamp Sparrow (*M. georgiana*)	224	4/29	11	Apr/May	−0.11	−0.05	0.69	−0.29	−0.88**	−1.11**
White-throated Sparrow (*Zonotrichia albicollis*)	441	4/20	11	Apr	0.24	−0.88	0.06	0.02	−0.29	−0.24*
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	410	5/17	13	May	0.17	0.00	−0.15	0.30	0.00	−0.22

TABLE 2. Continued.

Species	*n*	Median arrival	Range of medians	Temp range	Temp departure 0.1	Temp departure 0.25	Temp departure 0.5	NAO index 0.1	NAO index 0.25	NAO index 0.5
Indigo Bunting (*Passerina cyanea*)	207	5/12	16	May	0.84	0.22	0.58*	0.70	0.81	0.45
Bobolink (*Dolichonyx oryzivorus*)	349	5/15	7	May	−0.44	−0.36**	−0.43*	−0.15	−0.22	−0.21
Red-winged Blackbird (*Agelaius phoeniceus*)	507	3/23	19	Mar	−1.70	−2.38	−1.97	1.44**	0.83**	0.72**
Eastern Meadowlark (*Sturnella magna*)	251	4/19	35	Apr	0.17	0.28	−0.55	−1.92**	−1.10*	−1.20
Rusty Blackbird (*Euphagus carolinus*)	113	4/10	38	Apr	0.63	−1.70	−1.26	−0.66	0.37	0.06
Common Grackle (*Quiscalus quiscula*)	508	3/21	16	Mar	−1.57**	−1.53**	−0.99**	0.63	−0.25	0.07
Baltimore Oriole (*Icterus galbula*)	413	5/12	10	May	0.67**	−0.48**	−0.25	0.07	−0.11	0.13

with the expected negative slope between temperature deviation from the mean and arrival date. Four additional significant regressions had a positive slope. These likely arose by chance and are not considered further. The 0.25 quantile yielded the most significant relationships (30 of 105) while the 0.1 quantile produced 18 significant relationships, and the median quantile yielded 21 significant relationships.

Five species (Warbling Vireo, Ruby-crowned Kinglet, Northern Parula, Red-winged Blackbird, and Common Grackle) showed significant regressions for all three quantiles, demonstrating a strong response to spring temperatures. The regressions for two quantiles were significant for an additional 15 species. Eight of these species were parulids.

The results of the quantile regression analyses for the NAO index were similar to the temperature deviation regressions as only 63 of 315 regressions were statistically significant (Table 2). The 0.25 quantile had the greatest explanatory value, producing 25 significant regressions with negative slopes for the 105 species. The 0.1 and 0.5 quantile analyses yielded 18 and 20 significant relationships, respectively. The three significant regressions with positive slopes likely arose by chance.

Seven species (American Kestrel, American Woodcock, Belted Kingfisher, Eastern Phoebe, Tree Swallow, Ruby-crowned Kinglet, and Eastern Meadowlark) had significant relationships for all three quantiles. Twelve additional species had significant regressions for two of the three quantiles.

Only 45 of the 105 species failed to show a significant relationship for all six regressions. Thus, a minority of the species (42.9%) was unresponsive to some aspect of broad-scale temperature variability in their arrival.

DISCUSSION

Fundamental biotic changes are impelled by increasing global temperature. Abundant evidence of earlier leaf-out and flowering in vascular plants (e.g., Peñuelas et al. 2002) suggests phenological changes for pollinators, herbivores, and predators of herbivores. Responding to plant phenological changes, either by behavioral changes of individuals or population responses due to selection, should be relatively rapid for resident animals.

Finding the optimal schedule for departure from wintering areas, migration, and arrival in breeding areas is more complex for migratory species. Migratory birds may use higher than normal temperatures in wintering areas as a cue to begin migration. Some have argued that migrants may depart earlier than normal to avoid the physiological stress of high temperatures as summer approaches in areas used in winter. Alternatively, temperatures may be used as a predictor of earlier phenological events further north.

Migrant birds may migrate more rapidly if their appropriate food along their migratory pathway is phenologically advanced. This hypothesis seems reasonable but I know of no data on resource availability that can be used to test it with present knowledge. The strong correlation of spring temperatures from Maine south to Pennsylvania and New Jersey suggests there should be little difference in migration rate across that portion of the migratory route.

Ideally, migrant birds should respond to temperatures in breeding areas. Birds could then arrive sufficiently late to find adequate food for the metabolic demands of nesting and sufficiently early to compete for the best nesting sites. The difficulty is that birds have no way of predicting the climate from afar.

Quantifying changes in phenology provides one of the simplest means of assessing effects of global climate change on the biota of the earth. Phenologists can take advantage of stores of data on flowering dates, leaf-out dates, and nesting dates contributed by both professionals and amateur naturalists (Sparks and Menzel 2002). For example, Peñuelas et al. (2002) documented earlier leaf-out dates and later leaf-fall dates for vascular plants in the Mediterranean region from 1952 until 2000. On a broader scale, Parmesan and Yohe (2003) showed a global diagnostic fingerprint for 279 species.

For birds, global climate change has been invoked to explain earlier nesting in Tree Swallows (Dunn and Winkler 1999) throughout North America, and *Ficedula* flycatchers in Europe (Both et al. 2004) and India (Mitrus et al. 2005). However, the greatest amount of work on avian phenology with respect to global warming has been study of arrival dates of migratory birds. The data presented to date have shown strikingly different results. Wilson et al. (2000) documented no change in arrival date for migratory breeding birds in Maine between 1889–1911 and 1994–1997 while Peñuelas et al. (2002) showed that birds arrived at their Mediterranean site 15 days earlier in 2000 compared to 1952 (although lepidopterans appeared 11 days later).

At a local scale, Stervander et al. (2005) found a trend of earlier arrival (average of 0.9 day/decade) for 36 passerine migrants captured at Ottenby Bird Observatory in southeastern Sweden. They showed that arrival date was negatively correlated with the NAO index. Sokolov et al. (1998), at a banding station on the Courish Spit in the Baltic Sea, found a negative relationship between spring temperatures and late migrants (species arriving in May) but no relationships with earlier migrant species (those arriving in Apr). Mills (2005) analyzed data from Long Point Bird Observatory in Ontario, Canada over the period 1975 until 2000 and demonstrated that only 2 of 13 species analyzed had evidence of earlier arrivals through time. Töttrup et al. (2006) demonstrated birds were arriving 0.26 day/year earlier between 1976 and 1997 at a banding station on the Danish island of Christiansø.

Studies monitoring arrival dates by field observations also demonstrate changes in arrival date. Ledneva et al. (2004) found significant correlations of arrival dates at a farm in Massachusetts with spring temperatures. Bradley et al. (1999) reported that arrivals and first songs of several birds were earlier toward the end of a 61-year period at a single farm in Wisconsin. Tryjanowski et al. (2002) analyzed a data set spanning 1913 until 1996 at a farm in Poland and reported that 14 of 16 species of birds had a trend of earlier arrival dates over time. Each of these studies was based on a single, restricted site and any observed effects may have local rather than wide-scale explanations. One must extrapolate these results to the regional level with great caution.

Marra et al. (2005) avoided the problem of lack of replication (Hurlbert 1984) by analyzing data from three banding stations in North America. They demonstrated that birds migrated earlier in warmer springs (about 1 day for every 1° C increase in temperature). They were unable to show any relationships between arrival dates and the NAO index. Jonzén et al. (2006) used data from four banding sites in Scandinavia to show earlier recent arrival dates for a number of Scandinavian migratory breeding birds.

Analyses of arrival dates in a prescribed region may also avoid the problem of lack of replication (Sparks 1999). For example, Mason (1995) analyzed the arrival date records of the Leicestershire and Rutland Ornithological societies in Britain over a 50-year period and demonstrated earlier arrivals for 23 species in the latter part of the study period. Ptaskyk et al. (2003) demonstrated earlier arrivals for White Storks (*Ciconia ciconia*) from records collected across western Poland. Butler (2003) analyzed arrival date records from the Cayuga Lake region of New York and from central Massachusetts, and demonstrated that short-distance migrants arrived earlier in breeding areas in the later part of the 20th century compared to the first half. Long-distance migrants were influenced to a lesser extent by environmental warming.

The arrival date data from this study in Maine indicate modest temperature dependence (Table 2). For the median quantile, only 11 of 105 species had a significant relationship with temperature deviation. No weighting of the residual errors was used to produce the median quantile and, hence, this quantile is indicative of the entire population of first arrivals. Lower quantiles, biased toward early arrivals, resulted in a higher number of significant relationships (18 for the 0.1 quantile and 30 for the 0.25 quantile). Examination of the data indicates that only five species (American Woodcock, Warbling Vireo, Ruby-crowned Kinglet, Red-winged Blackbird, Common Grackle) had significant relationships for all three quantile regressions using temperature deviation as the predictor variable. The lack of concordance for the three quantiles for most species clearly indicates the heterogeneous variation across the statistical distribution.

Quantile regression analyses using the NAO index were similar with the 0.25 quantile producing 25 significant relationships. The median quantile analysis produced 20 significant relationships and the 0.1 quantile analysis only 18. Overall, only 20.0% of the regressions were significant. Seven species (American Kestrel, American Woodcock, Belted Kingfisher, Eastern Phoebe, Tree Swallow, Ruby-crowned Kinglet, and Eastern Meadowlark) had significant regressions for all three quantiles, demonstrating the heterogenous nature of the arrival data for most species.

Only 45 of the 105 species analyzed failed to have a significant result in at least one of the six regressions. The pattern is that temperatures, measured either by spring departures from the mean or by the NAO index, are not strong determinants of arrival date for migratory breeding birds in Maine. The percentage of regressions showing a statistically significant effect of spring temperatures on arrival date (21.0%) is quite similar to the value of 29% reported by Lehikoinen et al. (2004) in a meta-analysis of the effect of spring temperature on the arrival of common European migratory breeding birds.

Why do the data from this study show a weaker dependence of arrival data on spring temperatures than most other studies? One possible explanation is the data are not sufficiently accurate to show differences. This explanation can be rejected by examining the low variance around arrival dates for particular species. There were significant differences (ANOVA) among years for most species, indicating the between-year variance was not overwhelming the within-year variance. Furthermore, the sample size for each year for many species was based on more than 30 records (Table 2). Finally, the same type of data has been used by other workers who were able to show patterns of change in arrival date related to climate (Bradley et al. 1999, Butler 2003, Ledneva et al. 2004, Mills 2005).

A second and more compelling explanation is the migratory schedule for migratory breeding birds in Maine may be driven by photoperiod or some other environmental cue that has less variability than the year-to-year variability in spring temperatures (Coppack and Both 2002, Both 2007). This explanation is in accord with the results of Strode (2003) who demonstrated that seven species of wood warblers (Parulidae) are not arriving earlier in their breeding areas in Minnesota despite clear evidence that spring is now arriving earlier.

Those wood warblers are uncoupled from their food resources. Similarly, Pied Flycatchers (*Ficedula hypoleuca*) in the Netherlands have declined over the past two decades because their arrival in breeding areas has not changed while local phenological events, including caterpillar emergence, have advanced due to climate warming (Both et al. 2006). I have no doubt that dramatic change in Maine breeding birds will occur as global warming proceeds. However, the available data suggest the response in terms of arrival date, nesting date, and other phenological events will be gradual. Cold springs are not necessarily correlated with later arrivals for migratory birds in Maine (Table 2). Similarly, warm springs are not necessarily accompanied by earlier arrivals of migratory breeding birds.

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BREEDING PHENOLOGY AND SUCCESS OF BLACK SWIFTS IN BOX CANYON, OURAY, COLORADO

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ABSTRACT.—This study presents 11 years of nesting success and phenology data for Black Swifts (*Cypseloides niger*) at Box Canyon in Ouray, Colorado. Nest data were recorded on a near-daily basis for 160 nest attempts. Nesting success was 72% and mean and extreme dates of nesting events, including arrival, egg-laying, onset of incubation, hatching, and fledging are reported. On average, Black Swifts arrived on 13 June, egg laying started on 28 June, incubation started on 1 July, hatching occurred on 26 July, and fledging occurred on 13 September. The average incubation period was 26 days and the nestling phase was 48 days. In seven instances, a second egg appeared after loss of the first egg and, in one case, a third egg appeared. It was not possible to ascertain whether second or third eggs represented a renesting attempt or nest usurpation. *Received 23 August 2006. Accepted 4 March 2007.*

Nesting phenology and nest success rate information of Black Swift (*Cypseloides niger*) is currently based on small sample sizes. Precise nest habitat requirements cause nesting colonies to be widely scattered across appropriate landscapes, often in disjunct and remote areas. Through the 1900s, investigators found that Black Swifts nested in western North America at cool, moist, dark sites, usually associated with waterfalls. Colonies often consist of only one or two nesting pairs, making observation of large numbers of nesting birds logistically challenging. The cryptic nature of the nests and their frequent placement in inaccessible niches makes detection difficult; the long breeding season requires a large investment of time to observe nesting phenology. Despite these challenges, investigators have long been intrigued by the unique nesting characteristics and phenology of the species. Previous studies have indicated that, unlike all other North American swifts, Black Swifts produce single-egg clutches and have long incubation and fledgling periods (Lowther and Collins 2002). Previously published reports (Bailey and Neidrach 1965; Foerster 1987; Marín 1997, 1999; Boyle 1998; Hirshman 1998) on nests of this species consisted of small sample sizes ranging from observations of 4 to 35 nests with little or no information about nesting phenology.

From 1949 to 1958, O. A. Knorr surveyed areas of Colorado with suitable Black Swift nesting habitat to ascertain the species' nesting distribution and cataloged 27 colonies. In 1950, he discovered a colony of approximately 10 nesting pairs in Box Canyon in Ouray, Colorado (Knorr 1961). This easily accessible colony became popular with birdwatchers and is currently the largest known Black Swift colony in Colorado.

SEH logged more than 7,000 hrs from 1996 through 2006 observing nesting Black Swifts at the Box Canyon colony. Each year, arrival, nest building, egg laying, incubation, hatching, rearing, and fledging of the swifts were monitored. Her notes, including 196 season-long individual nest records, comprise the most extensive body of observations for this species. Retrospective review and analysis conducted on these data provide new information on the breeding biology of Black Swifts and allow for nesting phenology comparisons with previous studies of other populations. The objectives of this paper are to present phenology and nest success at the largest known colony of Black Swifts in Colorado.

METHODS

Study Site.—Box Canyon is <2 km southwest of Ouray, Colorado (38° 01′ 06″ N, 107° 40′ 44″ W) at an elevation of 2,380 m. Canyon Creek has formed a deeply incised, 60-m waterfall in the dark green diabase (dolerite) and quartzite rock layer (Gregory 1984) resulting in a narrow, deep canyon with the cliff of the

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falls forming a "box." The amount of water in Canyon Creek varies throughout the year based on snowfall, spring runoff, flash floods, and drought. The precipitous canyon walls provide nesting ledges and niches for Black Swifts. Spray from the falls, nearly continuous shade, and luxuriant growth of moss combine to form a cool, moist microhabitat perfect for nesting. Flash floods carrying boulders and woody debris periodically reconfigure the falls, causing the water and mist to shift position at the head of the falls, possibly changing nest microhabitats. Installation of new stairs and walkways in 1998 changed tourist traffic and viewing patterns, and may have influenced aerial access to some nest sites for the swifts.

Data Collection.—Observations occurred yearly for a total of 1,082 days from 1996 through 2006, averaging ~6 hrs/day from when swifts arrived at the falls until the last chick fledged. Observations generally alternated between mornings, afternoons, and early evenings, but some visits encompassed the entire day. During 11 years of observation, only 31 days (3%) had no observations.

Each nest was assigned a unique identification number in 1996, the first year of observation. New nests were assigned an alphanumeric label when found based on proximity to an existing nest (e.g., nest 6A is a new nest found near original nest 6). Nests were observed with 8 × 42 binoculars and a 20–40 × 60 tripod-mounted spotting scope. A handheld spotlight was used to illuminate nests and roosting sites during evening surveys.

We rated nests based on the observer's ability to view activity in the nest: (1) "excellent" indicates the nest, incubating adult, juvenile, and egg were visible under all conditions; (2) "good" indicates the nest, incubating adult, juvenile, and egg were detectable, but only under optimal natural lighting conditions; (3) "fair" denotes the nest, incubating adult, and older juvenile could be observed, but the egg and hatchling could not be seen and/or that the location was dark or misty; and (4) "poor" signifies that adults could be seen only flying to the site and/or only portions of the adult's body could be viewed during incubation, that juveniles could be seen only when they were large or were exercising wings prior to fledging, or that water, mist or darkness prevented good viewing. The designation for a nest changed in a few instances because nest edges were built-up so the observer could no longer see the nest contents or because construction of new walkways and stairs enabled the viewer to see the nest more clearly. Eight (31%) of 26 identified nests were "excellent", six nests (23%) were "good", three nests (12%) were "fair", and nine nests (34%) were rated as "poor" (Table 1).

Only events that were accurately viewed were included in our data analysis. Inferred, extrapolated or poorly observed events were not included. Only data from nests with "excellent" or "good" viewing designations (54% of nests) were used to ascertain dates of egg laying, onset of incubation, and hatching. Fledging dates used data from all successful nests, despite viewing designation, because these events were easily observed.

Arrival date was defined as the first observation of Black Swifts in the area. In late May and early June each year, SEH looked for Black Swifts by scanning the skies over Ouray and Box Canyon and, in some years, by visiting the colony site after dark for evidence of roosting birds.

Laying date was calculated as the average date the first egg was observed, and we included only nests in which the egg could be clearly seen. We also report laying date when nests with a second and third egg were included in the data analysis. We did not include laying dates for nests where the egg was first seen after incubation had begun.

Onset of incubation was defined as the date an adult was consistently incubating. Incubation period was the period starting with the day the adult was consistently on the nest until the day the chick was first observed. Hatching date was defined as the first day the chick was seen in the nest. Nestling stage was measured from the day the chick was first seen to the day the chick fledged. Fledging date was the date the nest was empty after having contained a near-fledging chick.

A nest attempt was defined as activity at a nest resulting in production of an egg (including second and third eggs) or as behavior indicating consistent incubation. Activity indicates interest in a nest without production of an egg, such as attendance at a nest by one or

TABLE 1. Nest presence and activity of Black Swifts at Box Canyon, Ouray, Colorado, 1996–2006.

Nest #	Year found	Years present	Status	Nest attempts	Years active	Years successful	Viewing designation
1	1996	7	Gone 2003	6	6	5	Excellent
1A	1997	4	Gone 2001	2	2	1	Poor in 1997, Good 1998–2000
1B	1998	3	Gone 1999; rebuilt 2004; gone 8 Jun 2006	3	3	3	Poor
2	1996	11	Present	9	9	6	Fair 1996–2004, Poor in 2005 and 2006
3	1996	7	Gone 2003	7	7	7	Good
4	1996	11	Present	12	11	10	Good
5	1996	11	Present	11	11	10	Poor
6	1996	11	Present	8	6	4	Excellent
6A	1998	9	Present	3	3	3	Poor
7	1996	11	Present	12	11	9	Excellent
7A	1996	11	Present	11	10	8	Excellent
8	1996	11	Present	10	10	7	Good
9	1996	10	Gone 6 May 2006	7	7	4	Good
9A	1998	9	Present	3	3	3	Poor
9B	1998	9	Present	9	9	7	Poor
10	1996	4	Gone 2000	4	2	1	Excellent
10A	1998	9	Present	10	9	5	Excellent
10AA	2006	1	Present	0	0	0	Excellent
10B	1998	9	Present	9	9	9	Good
10BB	2004	2	Present	2	2	2	Fair
10C	1999	7	Gone 13 Jun 2006	5	5	3	Fair
11	1996	2	Gone 1998	0	0	0	Excellent
12	1996	11	Present	7	7	4	Poor
12A	1997	2	Gone mid-1998	2	2	1	Poor
13	1998	7	Gone 2005	6	6	3	Poor
14	2003	3	Unsure if nest still present	1	1	1	Poor
Unknown[a]	1996	Unknown	Unknown	1	1	1	
Totals				160		117	

[a] Fledgling from an unknown nest was seen 15 September 1996 and reported to SEH after she had left Ouray.

more adults for a short period of time. Hatching success indicates the percentage of eggs that hatched. Fledgling success is the percentage of eggs hatched that fledged young. Nesting success refers to the percentage of nesting attempts that fledged chicks.

We calculated nest success and daily survival rates using the Mayfield method (Mayfield 1961, 1975) rather than apparent nest success (proportion of observed nesting attempts that succeed) to compensate for the possibility that some nests may have failed before they were discovered. Although observations were missed in only 3% of the Box Canyon breeding seasons, and SEH is an experienced observer, search frequency and investigator skill can distort apparent nest success results.

RESULTS

Nests were present at 26 individual sites in at least 1 year during 11 years of observation. Fourteen nests were identified in the initial year and 12 were built during the ensuing 10 seasons (Table 1). Eight of the original 14 nests persisted throughout the 11-year period; one of these was not known to be active. All remaining 25 nests had activity in at least 1 year. Of the 196 season-long individual nest observations made over 11 years, SEH recorded activity such as examination, repair, or roosting by adults or non-breeding birds that

TABLE 2. Nesting phenology of Black Swifts, Box Canyon, Ouray, Colorado, 1996–2006.

Event	Average date or number of days	Range of dates or days	Sample size	SD (days)
Arrival	13 Jun	31 May–19 Jun	11	6.6
Interval between arrival and egg laying	9 days	1–22 days	11	6.8
Egg laying (does not include 2nd and 3rd eggs laid)	28 Jun	19 Jun–16 Jul	73	5.4
Egg laying (includes 2nd and 3rd eggs laid)	30 Jun	19 Jun–29 Jul	81	7.1
Incubation onset	1 Jul	16 Jun–16 Jul	83	5.9
Incubation length	26 days	22–32 days	56	2.4
Hatching	26 Jul	17 Jul–9 Aug	59	5.6
Nestling phase	48 days	40–58 days	56	3.6
Fledging	13 Sep	31 Aug–7 Oct	117	7.3

did not result in egg laying at 18 nests and no activity was recorded at 26 nests.

The Mayfield nest success rate for 160 nest attempts over the 11-year period with 9,718 nest exposure days was 72% with a hatch rate of 82% and fledging rate of 90%. The daily nest survival rate was 0.996 (SE = 0.001). Thirty-five nest attempts failed over the observation period. The adult incubated an egg in 18 nests from 1 to 59 days (average 28 days) before it abandoned the egg or the egg disappeared. The chick died or disappeared in 10 nests prior to fledging, living from 3 to 34 days. Three nests were either destroyed or abandoned after flash floods. Multiple eggs were laid in four unsuccessful nests: two had two successive eggs, one had one egg and one successive chick that died at ~3 days of age, and one had three successive eggs. In nests with two eggs, the first egg disappeared after 1, 6, and 8 days. In the nest with three eggs, each egg disappeared the day after it was laid.

In addition to the three unsuccessful nests in which a second egg was laid, a chick was fledged from a second egg in three instances. The average laying date of a second egg (regardless of success) was 13 July (range = 6–28 July). An average lapse of 18 days (range = 11–37 days) occurred between laying of first and second eggs (n = 7) and a lapse of 12 days occurred between second and third eggs (n = 1).

Black Swift nesting phenology at Box Canyon indicated average arrival on 13 June (31 May–19 Jun) with egg laying starting by 28 June (19 Jun–16 Jul) and incubation starting on 1 July (16 Jun–16 Jul). Hatching occurred on 26 July (17 Jul–9 Aug) with fledging occurring on 13 September (31 Aug–7 Oct). The incubation period was 26 days (22–32 days) and nestling phase was 48 days (40–58 days) (Table 2, Fig. 1).

DISCUSSION

There is scant information published on nesting phenology of Black Swifts. Initial observations of Black Swifts in Box Canyon in 1996–1997 have previously been reported (Hirshman 1998). Boyle (1998) reviewed egg and hatching dates based on two published reports and only four data points collected during surveys for the Colorado Breeding Bird Atlas. Bailey and Niedrach (1965) reviewed all known nesting information, which at that time represented 35 individual nest reports in Colorado, only 13 of which had phenological events observed and recorded. Outside of Colorado, the most thorough Black Swift nesting studies were in southern California. Marín (1997, 1999) reported 20 direct field observations and reviewed 67 egg data cards, and Foerster (1987) observed breeding of 13–14 pairs over a 2-year period. Other studies presented extrapolated or estimated phenological events (Murphy 1951, Hunter and Baldwin 1962).

The inability to consistently view all nests in our study may have introduced some minor error in the data set. Many factors, including location and height of the nest, darkness, mist, and water affected how well nests could be observed. Eggs and small chicks could be difficult to view, whereas older, larger and more active chicks could be seen even in cases where earlier events at the nest could not be accurately observed. Length of brooding could not be precisely established due to viewing limitations.

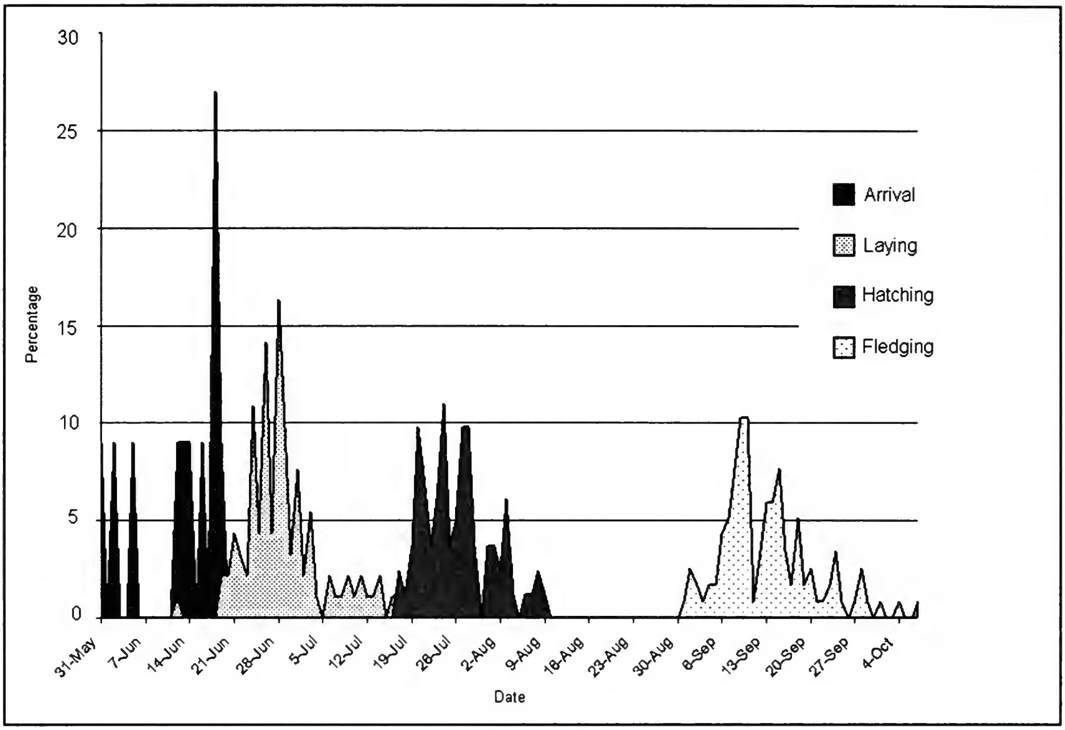

FIG. 1. Nesting phenology of Black Swifts, Box Canyon, Ouray, Colorado, 1996–2006.

The Mayfield nest success rate (72%) was similar to the apparent nest success rate of 73% (95% CL: 65–79%). The Mayfield method also produced a hatch rate and a fledging rate <1% different from the apparent rates (81.8 vs. 81.3% and 89.8 vs. 90.0%, respectively). These similarities suggest that few, if any, nesting events were not detected near the time of occurrence.

The Mayfield method nest success reported here (72%) is slightly lower than that reported by Foerster (1987) who measured an apparent rate of 80% (*n* = 20) over a 2-year period. Fledgling success at Box Canyon (90%) was lower than the 95% apparent rate reported by Foerster (1987). In the Hunter and Baldwin study (1962), two of the five nests failed during the early nestling period. Fledgling success rate at Box Canyon in 2002, during the worst drought in recorded history, was 52%. Excluding 2002, the fledgling success rate at Box Canyon over the remaining 10 years was 93%. Hatching success at Box Canyon (82%) was similar to the 81% (*n* = 16) reported from southern California (Marín 1997).

Black Swift arrival dates had a wider variation than might be expected. Some variation may be attributed to regional weather and food availability. Finding swifts by inspecting the sky is also somewhat dependent on luck. Swifts fly quickly and their presence in the skies can be easily overlooked. Inspecting roost sites in 2004, 2005, and 2006 at Box Canyon after dark revealed the birds' presence 10–16 days earlier than had been observed in previous years, suggesting that direct inspection of known roost/nest sites is probably a more accurate method to ascertain arrival date.

Overall, the interval between arrival of swifts and onset of egg laying averaged 9 days. However, in the first 8 years of the study, arrival of swifts was recorded by seeing the adults flying over the colony site during the day, resulting in an interval of 6.5 days. We believe this method is not as accurate as inspecting the colony nesting site at night. During the last 3 years of observation, using the latter technique produced an interval of 16 days, indicating that swifts may have a longer interval between arrival and laying than previously calculated. The delay is probably attributable to formation or reaffirmation of pair bonds, courtship displays, mating, inspection and selection of nest sites, and refurbishing or rebuilding of nests. Energetics, food availability, and environmental influences such as temperature and precipitation may affect length of this interval.

SEH observed repair of existing nests or complete rebuilding of nests at sites where previous nests had disappeared in four instances. Nest-building activities took 13–15 days. SEH did not observe building of a new nest and most nest-building activity apparently occurred early or late in the day, outside of observation periods. Marín (1997) observed nest building only once, but no time period was given. However, he refers to an egg data card indicating a nest was built in 4 days. Lowther and Collins (2002) provide no information for nest building.

On average, incubation began 3 days after laying. In a few cases, incubation started the day of laying, while in others it was delayed up to 7 days. Incubation periods reported by Marín (1997) averaged 24 days (range = 23–26, n = 6). Legg (1956) reported a 27-day incubation period (n = 1), and Murphy (1951) estimated incubation to be 24 days (n = 1). These dates generally agree with the average 26-day incubation period found in this study (n = 56).

The variation in length (40–58 days) of the nestling stage is difficult to explain. The duration of nestling stage may be a phenotypic plastic life history trait in Black Swifts. Eggs and nestlings of swifts in the Family Apodidae are resistant to cooling, and nestlings can go into torpor to conserve energy (Camfield 2004), especially when adults are away on feeding forays. During torpor, which is also influenced in intensity by the nest's microclimate, metabolism decreases and possibly influences the chick's growth, contributing to the wide variation in the nestling stage. Nestling growth is also affected by weather, since adult foraging success and subsequent feeding frequencies of the chick depend on insect swarms (Camfield 2004). Foerster (1987) reported a nestling period averaging 48 days (n = 14), with a range of 45 to 51 days. Marín (1997) reported an average nestling period of 48 days (n = 9) in his 3-year study, and Legg (1956) reported a nestling period of 45 days for one chick. A second source of variation in nestling stage could be caused by difficulties in viewing the hatching event. Despite using only nests with "excellent" or "good" viewing designations, identification of the exact day of hatching can be difficult.

Black Swift nests were relatively persistent within the colony, some lasting 11 years, although most received repairs each year (Table 1). A nest's longevity depends on its location, how sheltered it is from weather and runoff from the falls, whether it receives any repair, and the durability of construction and materials. Of 196 season-long nest observations at 25 nest sites over 11 years, 178 (91%) recorded either nest attempts (n = 160) or activities that did not result in egg laying (n = 18). Thus, most nests receive some attention by pairs in most years. This activity may indicate that available nest and roost sites in Box Canyon are or nearly are saturated.

Causes of nest failure are difficult to accurately identify. Most avian species abandon their eggs during incubation when foraging becomes difficult or when their energy reserves dwindle to critical levels (Gill 1994). Other causes of nest failure include loss of one of the adults, infertile or otherwise defective eggs, environmental causes such as flash floods, disturbance due to human activity, parasites and disease, displacement of nestlings from the nest, and improper microhabitat at the nest. No predation was observed at Box Canyon, but terrestrial and aerial predators could be a cause of nest failure in other colonies. American Crows (*Corvus brachyrhynchos*), Common Ravens (*C. corax*), and Steller's Jays (*Cyanocitta stelleri*) occasionally were seen to approach the mouth of the canyon, but none has been observed entering or approaching the swift nests.

Disappearance of eggs during incubation and early abandonment of the nest by adults have been noted by others (Hunter and Baldwin 1962, Foerster 1987, Marin 1997). All nests at Box Canyon are out of reach of site visitors, and no terrestrial or aerial predation has been observed. Foerster (1987) reported a rock being thrown at a nest as cause for egg breakage, and this cannot be dismissed as a possibility at Box Canyon. Visitation at this site from 1997 to 2004 averaged 57,781 people annually (Box Canyon Falls Park 2005). It is also possible an egg could be pushed from the nest by the adult swifts, either intentionally or accidentally, or removed from the nest by an antagonistic conspecific.

Possible causes for chick loss include disease, ectoparasites, lack of proper brooding, starvation, desertion, improper nest microhabitat (too wet, too dry, too cold or too hot), and displacement from the nest prior to fledging. Hunter and Baldwin (1962) reviewed the existing accounts of nesting and noted a large proportion of nesting failures involved mysterious disappearance of the young, young found dead in the nest, or young falling from the nest. Knorr (1961) observed a chick falling from a nest and being swept away in a stream. In three instances, SEH or others found chicks on the ground near the nest site. In 2005, a chick fell from its nest and was returned to the nest with the aid of a 3-m metal pole wrapped with cloth to which the chick could cling; the chick successfully fledged 13 days later. In 2004, a chick spent 2 days on the canyon floor and was attended by an adult. SEH placed this chick in a crack on the canyon wall from which it fledged a few days later. In 2003, a new nest site was discovered only after the chick from that nest was found on the canyon floor, probably the result of an unsuccessful fledging attempt. The chick was placed near the newly discovered nest and it fledged the following day. These observations suggest that young falling from nests may significantly contribute to nesting attempt failure in Black Swifts.

Of the 35 instances in which a nest attempt failed, egg replacement occurred seven times (20%), and a third egg was laid once (2%). The latest date of appearance of a second egg from which a chick was successfully raised was 28 July; the chick fledged on 7 October. Marín twice observed loss of eggs without replacement eggs being laid and stated, "The Black Swift lays a single egg, and if this egg is lost, there is no attempt to replace it" (Marín 1997:302). Using banded birds during the breeding seasons of 1999 and 2000, Marín observed four nests in which a second egg was laid and in all cases the replacement egg was laid not by the original female, but by other females from the colony or a different colony, usually younger females (M. Marín, unpubl. data). Foerster (1987) reported clutch size to be one egg in all cases and did not observe replacement eggs. It is not known why a second egg is laid in some instances of loss or failure of the first egg and not in others. Ability to renest depends upon food supplies, accumulated reserves and nutritional status of the female, mating opportunities, nest availability and microclimate, and continued help by mates. The amount of energy invested in a first nesting attempt and lateness of the season (effects of photoperiod) can further influence renesting (Gill 1994).

Our observations generally agree with those of other investigators that once young fledge, both young and adults leave the colony. However, during a bout of inclement weather, one chick that fledged in the early morning and was gone all day returned to roost at its nest one more night. It is believed that young of many swift species fledge in the morning before 0800 hrs (Lack 1973, Marín 1997). The majority of the swifts in our study fledged between 1600 hrs on one day and 0800 hrs the following morning. However, seven chicks were observed to fledge between 0900 and 1840 hrs.

Relationships between nesting success and weather elements such as temperature and precipitation are often obscure. The study period included the most severe drought experienced in the area in more than a century (Western Regional Climate Center 2005). The 11-year observation period was too short and provided a sample size too small to develop statistically significant results correlating weather and nesting success. Although the poor nest success rate of 2002 (50%) coincided with the worst year of drought, the rate was 44% in 2006, a year of near-normal precipitation. Most nests (5 of 7) failed in the nestling phase during the 2002 drought year, and all nest failures (6) in 2006 occurred during the incubation stage. These differences suggest the cause of nest failures differed between years.

The Black Swift colony at Box Canyon has apparently remained stable or perhaps even increased over 57 years. Nest site fidelity is one attribute, along with adult longevity, believed to be responsible for long-term traditional nest site use noted for this species (Collins and Foerster 1995).

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GROWTH AND DEVELOPMENT OF THE MARIANA SWIFTLET

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ABSTRACT.—The Mariana Swiftlet (*Aerodramus bartschi*) on Saipan lays a single white egg which is incubated for 22.95 days (range 17–30 days). Newly hatched nestlings are naked and weigh 1.11 g (range 1.0–1.2 g). Nestlings grow slowly, reaching asymptotic weight on day 29 and fledging after 46.8 days (range 40–55 days). Post-asymptotic weight recession is ±2% and nestlings fledge at slightly above adult weight of 8.01 g. Wing and tail length are >94% of adult size at fledging. Low clutch size, slow chick growth, and extended nestling period are characteristic of other species of swiftlets and may represent food limitation in these diminutive aerial insectivores. *Received 25 September 2006. Accepted 24 February 2007.*

The cave swiftlets (Apodidae: Collocaliini) are widespread in the Indo-Australian region from the Seychelles to Tahiti, the Marquesas, and Micronesia (Medway 1966, Chantler 1995). They are well known for their ability to echolocate (Medway and Pye 1977, Collins and Murphy 1993, Price et al. 2005) and for producing the highly prized edible nests used in Chinese cuisine and medicine (Chasen 1931, Medway 1963, Lim and Cranbrook 2002, Nguyen Quang et al. 2002). These diminutive swifts are, in many cases, phenotypically similar with geographically separated insular populations making species and subspecies delineations difficult (Mayr 1937). More recent reviews using DNA sequence data have clarified some of the relationships in this group (Lee et al. 1996, Clayton and Johnson 2000, Price et al. 2005, Thomassen et al. 2005).

In the Mariana Islands, the population *bartschi* was formerly considered a subspecies of the widespread Vanikoro Swiftlet (*Aerodramus vanikorensis*) (Pratt 1986, Pratt et al. 1987, USDI 1991). This was based largely on nest structure and morphology (Medway 1966). However, it has also been considered a subspecies of the Caroline Swiftlet (*A. inquietus*) of the Caroline Islands or a separate species, the Guam Swiftlet (*A. bartschi*) (Browning 1993, AOU 1998); its common name was subsequently changed to Mariana Swiftlet (*A. bartschi*) (Banks et al. 2002). Recent DNA studies support its specific distinctness and suggest it is a sister species to Sawtell's Swiftlet (*A. sawtelli*) of the Cook Islands (Lee et al. 1996, Thomassen et al. 2005).

The Mariana Swiftlet is currently a federally listed endangered species throughout the Mariana Islands with about 5,000 individuals on Saipan (V. A. Camacho, unpubl. data) and a few hundred birds on both Guam and Aguijan. It is extirpated from Rota and Tinian. A small introduced population of the Mariana Swiftlet exists in Halava Valley, Oahu, Hawaii (AOU 1998, Wiles and Woodside 1999).

The breeding biology of several swiftlet species has been extensively studied (Medway 1962a, 1962b; Tarburton 1986; Bryant and Tatner 1990), particularly those that produce highly valued edible nests (Langham 1980, Nguyen Quang 1992, Lee and Kang 1994, Lim and Cranbrook 2002, Nguyen Quang et al. 2002). However, data on the growth of nestling swiftlets are currently available for only six species (Langham 1980; Tarburton 1987a, 1990, 1993a, 2003; Bryant and Tatner 1990; Lee and Kang 1994). Our objective is to present similar data on nestling growth as part of the recovery program for the endangered Mariana Swiftlet.

METHODS

This study was conducted in the 1987 to 1990 breeding seasons on Saipan (15° 12′ N, 145° 43′ E), a 123-km^2 island of coralline limestone in the Commonwealth of the North-

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ern Mariana Islands. The climate of Saipan is tropical with temperatures remaining between 22 and 33° C. Annual rainfall averages ~2,000 mm, most of which occurs between July and November (van der Brug 1985); a dry season occurs from December to May, when monthly rainfall averages 92.7 mm. The plant communities of Saipan have been described by Fosberg (1960).

Measurements of 162 nestlings at the Navy Hill Cave, 1.5 km east of Garapan, were supplemented by measurements of five nestlings at Celis Cave, 5 km southeast of Garapan (USDI 1991). Nests were checked with a pole-mounted mirror; an extension ladder was used to retrieve eggs and nestlings for measurement. Nestlings were weighed and measured only 1–5 times (2.36 ± 0.9) ($\bar{x}$ ± SD) at intervals that averaged 11.45 (±4.2) days to minimize colony disturbance. Wing length was measured to the nearest 1.0 mm with a flexible plastic ruler and weights were obtained to the nearest 0.1 g with a Pesola spring balance. Eggs were measured with dial calipers. Individuals were banded with USGS Bird Banding Laboratory numbered aluminum bands for identification. Hatching and fledging dates were assumed to be the midpoint between the earliest and latest possible dates based on visitations. Mean incubation interval and age at fledging were taken from subsets of nests with ≤5-day gaps between observations. Nine nestlings were 1–2 days of age when first examined and were re-examined on 2–4 occasions up to the age of 25 days. Nestlings of unknown age were classified by comparison of their wing lengths on one or more occasions during the period of linear wing growth when 12 to 35 days of age (Lee and Kang 1994). Statistical analysis of the data was performed using a computer program that fits values to the Richards Growth Model (Bradley et al. 1984). Variables calculated were: (1) asymptotic mass, (2) weighted mean growth rate per day, (3) age at inflection point of the sigmoid growth curve when growth was maximal, (4) percent of asymptotic mass at inflection, (5) time from 10 to 90% ($t_{10\text{–}90}$) of the asymptote, and (6) the shape parameter (Brisbin et al. 1987). Data for other swiftlets (Lee and Kang 1994) were fitted to the Logistic Growth Model where the shape parameter is fixed at 2.0; in the Richards Growth Model the shape parameter is variable (Brisbin et al. 1987)

RESULTS

All reported clutches of the Mariana Swiftlet in Saipan (n = 404) were of a single white egg. The eggs were 18.21 ± 0.55 ($\bar{x}$ ± SD) mm in length (range 17.0–19.7, n = 106), 12.05 ± 0.40 mm in width (range 10.3–13.0), and weighed 1.37 ± 0.14 g (range 0.8–1.6, n = 90). Mean incubation duration for 22 eggs on Saipan was 22.95 days and ranged from 17 to 30 days.

Newly hatched nestlings were pink skinned and naked, devoid of any natal down. Pin feathers could be seen as dots beneath the skin on the dorsum and wings by day 4–6 after hatching and were visible on all tracts by day 9. Pin feathers erupted through the skin starting about day 13; the feathers began emerging from their sheaths by day 17–19. The eyes were open by day 20–21. Contour feathers were about 60% emerged by day 28–30 and flight feathers were about 50% emerged by day 37. Nestlings were fully feathered and capable of short flights by day 45–47 and, on average, fledged by day 47, although at least one remained in the nest until day 55.

Sixty data points for wing length and body mass were obtained from 25 nestlings in 1988 and 107 data points were obtained from 50 nestlings in 1989. Mariana Swiftlet nestlings grew similarly in both years with 95% confidence intervals for three of the growth parameters widely overlapping (Table 1). Thus, data for both years were pooled in this analysis.

The wing was 6 mm long at hatching and grew slowly until the primary pin feathers erupted at day 12–13. The wing increased in length in a linear fashion from day 13 to day 45 (Fig. 1) when it was about 100 mm or about 94% of the adult wing length of 106 ± 2.78 ($\bar{x}$ ± SD) mm (range 102–112, n = 29). Tail length increased linearly from day 15 to day 45 (Fig. 1). Tail length at fledging closely approximated adult length of 50.5 ± 1.76 mm (range 46–56, n = 26).

Nestlings on day 1 weighed 1.11 ± 0.06 ($\bar{x}$ ± SD) g (range 1.0–1.2, n = 8). Thereafter, nestlings grew slowly, reaching asymptotic weight of 8.21 g at day 29; the time from 10 to 90% of asymptotic size ($t_{10\text{–}90}$) was 20.28 days (Table 1). There was only slight (±2%)

TABLE 1. Growth parameters for Mariana Swiftlets. Data are for 1988 and 1989 separately and combined. The data are fit to the Richards Curve (Bradley et al. 1984) with bootstrapped 95% confidence intervals (CI).

Parameter	1988	1989	1988–1989
Individuals (*n*)	25	50	75
Data points (*n*)	60	107	167
Asymptotic size (AS) (g)	7.98	8.19	8.21
95% CI (g)	7.18–8.88	7.85–8.54	7.95–8.48
Weighted mean growth rate (g/day)	0.542	0.432	0.406
Time to inflection (days)	10.51	11.34	11.10
% of Asymptotic size at inflection	0.622	0.627	0.611
95% CI (%)	0.35–0.83	0.45–0.77	0.51–0.70
Shape parameter	3.83	3.29	3.60
T_{10-90}	13.98	17.97	17.59
95% CI	7.69–25.44	16.04–20.14	16.10–19.22

post-asymptotic weight recession (Fig. 2) and nestlings fledged after 46.83 days (range 40–55 days) at slightly higher than adult weight of 8.01 ± 0.77 g (5.4–10.4, *n* = 28).

DISCUSSION

Mariana Swiftlet nests are made of plant material and glued to cave walls by copious sticky saliva. The principal nest material in Guam is *Neckeropsis lepiniana*, a moss that is abundant in forest areas near the nest caves (Jenkins 1983). The cone shaped nests were 50–60 mm wide, 65–70 mm in length with a shallow cup about 10 mm deep (Drahos 1977, Jenkins 1983). Nests in Saipan were different in their size and placement from those in Guam (D. W. Stinson, unpubl. data).

The incubation period and age at fledging of Mariana Swiftlets are similar to those recorded for other swiftlets, including those with single and two-egg clutches (Table 2). Mariana Swiftlet nestlings are devoid of natal

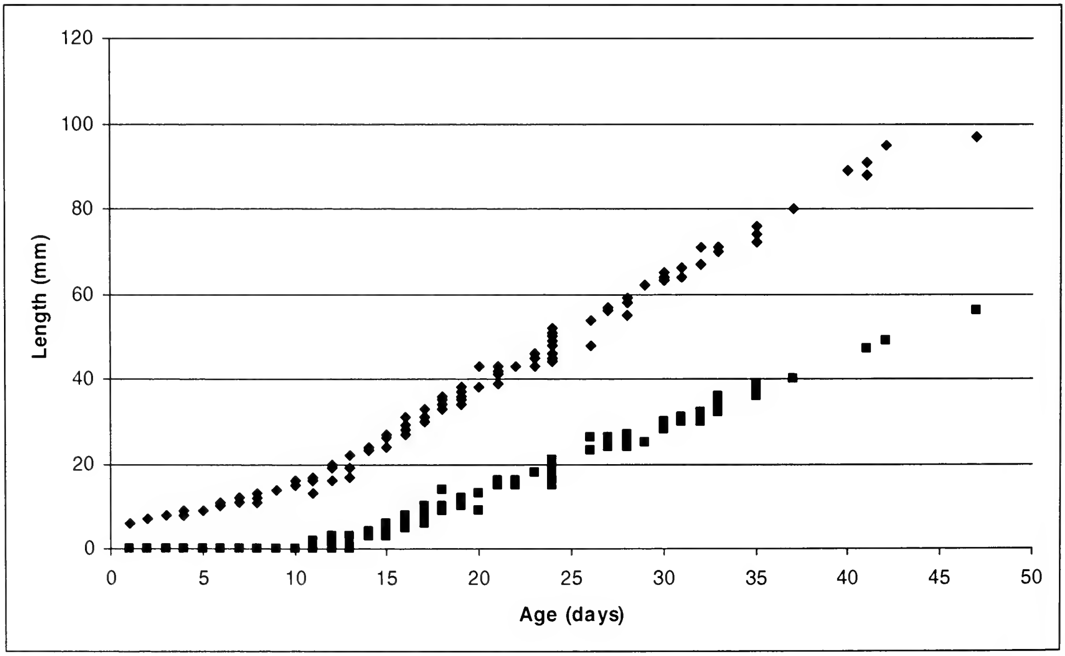

FIG. 1. Growth of the wing (closed diamonds) and tail (closed squares) of Mariana Swiftlet chicks in Saipan in 1988 and 1989. Mean adult wing length is 106 mm and tail length is 50.5 mm.

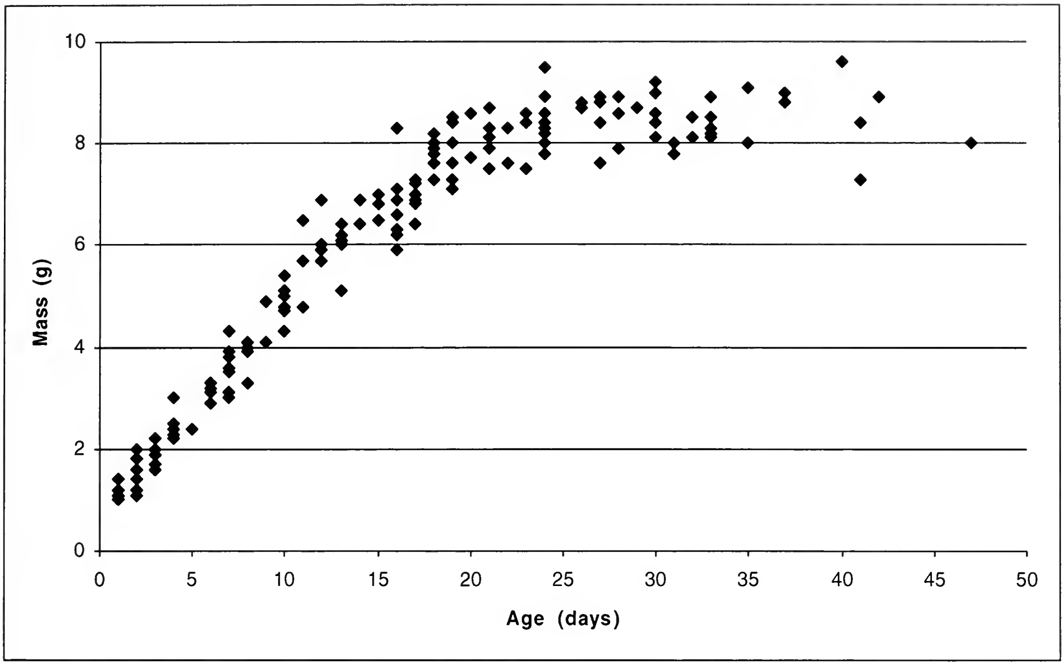

FIG. 2. Growth of Mariana Swiftlet chicks in Saipan in 1988 and 1989. Mean adult body mass is 8.01 g.

down as in all species in the Apodidae (Collins 1978). Nestlings grow slowly and have a nearly 7-week fledgling period (Fig. 2). It is possible this represents a K-selected strategy with a low reproductive rate and slow growth rate of young. Some, but not all, nest sites are secure (in caves) from many predators possibly reducing selection for rapid growth. Annual productivity may be curtailed to optimize lifetime reproduction. Unfortunately, there are no data on long-term survival of adult Mariana Swiftlets. Elsewhere, White-rumped Swiftlets (*Aerodramus spodiopygius*) in Fiji are long-lived, reaching ages of 9–12 years (Tarburton 1987b). It is also possible that Mariana Swiftlets, and perhaps other swiftlets, are food limited which is reflected by low clutch size and slow growth rate of the nestlings. Other possible causes of the low clutch size, such as nest size, predation, and molt have been reviewed elsewhere (Tarburton 1993a).

Variation in quality of the diet has been shown under experimental conditions to influ-

TABLE 2. Reproductive parameters ($\bar{x}$ ± SD) (range) of six species of swiftlets.

Species	Incubation period (days)	Age at fledging (days)	Clutch size	[a]Source and location
Mariana Swiftlet (*Aerodramus bartschi*)	22.95 (17–31)	47 (40–58)	1	(1) Saipan
White-nest Swiftlet (*A. fuciphagus*)	25.1 ± 0.3	39.8 ± 2.6	2	(2) Singapore
White-nest Swiftlet	23.0 ± 3.0 (20–29)	43.0 ± 6.0	2	(3) Malaysia
Black-nest Swiftlet (*A. maximus*)	25.5 ± 2.2	45.9 ± 2.6	1	(2) Singapore
Black-nest Swiftlet	28.0 (21–39)	58.5 (44–77)	1	(4) Sarawak
Mossy-nest Swiftlet (*A. vanikorensis*)	23.0 (21–28)	48.5 (31–57)	1–2	(4) Sarawak
White-rumped Swiftlet (*A. spodiopygius*)	23.0	46.0	2	(5) Fiji
Mountain Swiftlet (*A. hirundinaceus*)	?	(67–74)	1	(6) New Guinea
Sawtell's Swiftlet (*A. sawtelli*)	±27	53.3 ± 1.2	2	(7) Cook Is.
Glossy Swiftlet (*Collocalia esculenta*)	21.5 (20–28)	42 (41–58)	2	(4) Sarawak

[a] Sources: (1) = this study, (2) = Lee and Kang 1994, (3) = Langham 1980, (4) = Medway 1962a, (5) = Tarburton 1986, (6) = Tarburton 2003, and (7) = Tarburton 1990.

ence nestling growth (Boag 1987, Johnston 1993). However, aerial insectivores (Apodidae, Hirundinidae) have been shown to take a wide variety of prey taxa from differing habitats (Collins 1968, 1980; Turner 1982; Tarburton 1993b; Rudalevige et al. 2004). This makes it unlikely that variation in representation of any one prey component would influence the overall quality of their diet (Johnston 1993). The aerial arthropod prey of both swifts and swallows contain large amounts of protein and other nutrients (Turner 1982). It is more likely the factor limiting nestling growth in these birds would be food energy supply in the form of insect prey abundance and not nutritional quality (Johnston 1993).

Weather patterns, particularly wind and rain, exert strong influences on quantity of food available for aerial insectivores (Turner 1982). There is a peak in Mariana Swiftlet reproduction (egg laying) in the last half of the dry season (May) into the first half of the wet season (Sep) (Reichel and Camacho 1989, Rice 1993). This presumably relates to the period of maximal availability of insect food resources to support breeding; no data on aerial insect seasonal abundance in Saipan are available. In his study of three species of swiftlets in Sarawak, Medway (1962b:243) noted there was "evidence of a broad annual fluctuation in food supplies". Similarly, Tarburton (1993a, 1993b) noted annual differences in food availability at two study locations in Australia and Fiji. Day-to-day differences in food availability have been noted even in years with good food supplies; periods of strong rains disrupt foraging and decrease the amount of aerial insect prey brought to nestlings (Medway 1962b, Tarburton 1993a). This may explain the curtailment of Mariana Swiftlet breeding during the height of the wet season when heavy rains would depress aerial insect food resources and swiftlet foraging time. The limitation in time in Australia, during which food resources are sufficient to support swiftlet reproduction, has necessitated overlapping of sequential broods to have reproduction and transient resources coincide (Tarburton and Minot 1987).

Food availability and adult foraging capacity can be studied by experimental enlargement of clutch or brood size. This has not been attempted for Mariana Swiftlets. However, White-rumped Swiftlets in Australia and Fiji showed a decrease in rate of nestling weight gain and wing growth in experimentally enlarged broods (Tarburton 1987a, 1993a), particularly in less suitable (dry) years when they are "struggling to adequately feed one nestling" (Tarburton 1993a:174). Black-nest Swiftlets (*A. maximus*), in Singapore, but not White-nest Swiftlets (*A. fuciphagus*), showed higher nestling mortality in enlarged broods (Lee and Kang 1994). Similarly, the older nestling in asynchronously hatching broods of two in the White-bellied Swiftlet (*Collocalia esculenta*) in Malaysia grew more rapidly than its late-hatching brood mate; single brood nestlings were, on average, heavier than those in artificially synchronous broods of two (Bryant and Tatner 1990). In this case, and in *A. fuciphagus* which also lays a clutch of two, the second egg and nestling may be more of a hedge against total reproductive failure should something happen to the first nestling (Lee and Kang 1994).

Further support for the food limitation hypothesis in Mariana Swiftlets can be gained from examination of the trajectories of weight gain of the nestlings. Nestling growth of Mariana Swiftlets and other swiftlets is typically slower than in other Apodidae and post-asymptotic weight recession is minimal (<10%; estimated from Langham 1980, Bryant and Tatner 1990, Tarburton 1993a, Lee and Kang 1994). Nestlings of 10 species of swifts (Collins 1968; Ricklefs 1968; C. T. Collins, unpubl. data) and Barn Swallows (*Hirundo rustica*; Ricklefs 1968, George and Al-Rawy 1970) grew more rapidly and reached asymptotic weight 10–25% above that of adults and then had substantial weight recession prior to fledging at close to adult weight. Most of the observed weight recession in swifts, and also swallows, represents a decrease in water content of the integument (skin and growing feathers) (Ricklefs 1968). Studies of the Common Swift (*Apus apus*) in Europe showed that in bad resource years, asymptotic weight of nestlings was lower and achieved up to 10 days later with less pronounced weight recession although weights at fledging were similar (Lack and Lack 1951, Pellantova 1981). The overall growth trajectory in these years was lower and there was a marked similarity to that seen in Mariana Swiftlets. It is unlikely the observed lower growth trajectory in both Common Swifts and Mariana Swiftlets was due to a difference in integumental or developing feather water content as the plumage in these birds appeared to grow normally. It would appear the difference is due to slower development of muscle and organ systems. It also indicates that Mariana Swiftlets are unable to accumulate lipid reserves used by other swifts and swallows as a hedge against short-term variation in aerial prey abundance affecting nestling growth (O'Connor 1977, Johnston 1993). Swiftlets, because of their small size, are constrained to feed on small insects (predominantly <5 mm long; Tarburton 1993b; C. T. Collins, unpubl. data). Insects in this size range are numerically abundant, except perhaps during periods of heavy rainfall, but they do not have a high caloric content. Thus, Mariana Swiftlets, and possibly other swiftlets as well, may face chronic conditions of low energy intake which constrain both clutch size and nestling growth rate.

Further studies of Mariana Swiftlet nestling growth combined with quantification of both feeding rates, and amount and caloric density of food delivered will be needed to more clearly define the selective pressures leading to low clutch size and growth rate in these and other swiftlets.

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WOOD THRUSH NESTS IN DENSE UNDERSTORY MAY BE VULNERABLE TO PREDATORS

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ABSTRACT.—We used Mayfield logistic regression and an information-theoretic approach to examine habitat characteristics associated with nesting success of Wood Thrushes (*Hylocichla mustelina*) across an urban to forested gradient in southwestern Pennsylvania in 2003 and 2004. Both nest placement and number of understory stems provided equally plausible models. Mayfield success was 20% higher for nests >3 m above ground level while dense understory was associated with low nest height. Wood Thrush nests in the forest interior averaged 2 m higher with a third less understory than edge nests. Urbanization and distance to the forest edge were not useful predictors of Wood Thrush nest success. The analysis was confounded by low breeding density at the most urbanized sites, but we found moderate success (42%, $n = 63$) across a fragmented landscape with minimal core forest area. Interior nests in a large contiguous forest were twice as successful (60%, $n = 31$) compared to edge nests (25%, $n = 33$) adjacent to a small housing development. We do not know the mechanism underlying increased predation of low understory nest sites that we observed. The ability of Wood Thrushes to see and/or effectively attack a predator in the area may be important for nest defense; changes in the predator community associated with forest edges may also explain differences in nest success. The relationship between nest placement, nest defense, and the predator community needs further study. *Received 28 March 2005. Accepted 15 January 2007.*

Developing management plans to protect Nearctic-neotropical migratory songbirds in breeding areas requires understanding of the complicated factors that influence nesting success (Martin 1992, Driscoll et al. 2005). Nest predation associated with habitat fragmentation remains one of the threats implicated in declines of forest-interior nesting species. Forest fragmentation can increase predation on nesting birds by creating edges adjacent to another habitat type (Gates and Gysel 1978, Batáry and Báldi 2004) and decreasing the amount of forested area in the surrounding landscape (Donovan et al. 1995, Robinson et al. 1995). Generally, the underlying mechanism driving predation in fragmented forests is linked to increased abundance, activity, or species richness of nest predators associated with heterogeneous habitats (Chalfoun et al. 2002b).

The Wood Thrush (*Hylocichla mustelina*) has been studied as a model species to examine the effects of forest fragmentation across a range of geographic locations (e.g., Donovan et al. 1995, Hoover et al. 1995, Robinson et al. 1995, Weinberg and Roth 1998, Friesen et al. 1999, Fauth 2000, Driscoll and Donovan 2004, Driscoll et al. 2005, Phillips et al. 2005). Long-term population decline has made the Wood Thrush a species of conservation concern (Sauer et al. 2004). Wood Thrushes breed both in the interior and on the edges of a wide variety of mesic forest habitats (Roth et al. 1996). This species typically is double-brooded and will renest multiple times if the nest is depredated. Thus, sufficient samples of active nests can be found to study factors influencing nesting success. However, estimates of nesting success should not be equated with annual productivity or population dynamics (Grzybowski and Pease 2005).

Urbanization is rapidly expanding in the United States with increasing human populations (Lubowski et al. 2006), but there is little known about the effects of urbanization on nesting success of forest-interior species. Increased predation in urban as opposed to agricultural areas was found in a highly fragmented landscape in Ohio (Bakermans and Rodewald 2006). Results are contradictory for the influence of housing density on Wood Thrush nesting success (Phillips et al. 2005). Urbanization effects would generally be driven by changes in the nest predator community (Danielson et al. 1997, Bakermans 2003). Changing predator communities in urbanized areas could alter the safety of microhabitat

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and nest-site characteristics that forest-interior species have evolved to select (Martin 1988, 1998). Wood Thrushes breed in closed-canopy mature forest (Bertin 1977, James et al. 1984) and nest sites are selected in areas with dense understory (Hughes 1977, Hoover and Brittingham 1998, Artman and Downhower 2003). Some studies suggest that nest placement may make nests less accessible to predators and/or improve nest defense (Wilson and Cooper 1998, Schmidt and Whelan 1999) while concealment may make the nest difficult to detect, especially if predators are visually oriented (Johnson 1997). The interaction between and relative importance of nest microhabitat, forest edge, and the effects of different landscape types are only beginning to be identified (Rodewald and Yahner 2001, Driscoll and Donovan 2004, Driscoll et al. 2005, Bakermans and Rodewald 2006).

We studied the effects of forest fragmentation on Wood Thrush nesting success across an urban (i.e., residential or commercial areas) to forested gradient in southwestern Pennsylvania. This continuum typically occurs around metropolitan areas in the Mid-Atlantic region with suburban residential areas spreading into a predominantly forested landscape. Our objective was to identify habitat characteristics associated with Wood Thrush nesting success. We focused on landscape level, forest edge or vegetation factors that might be manipulated through forest management (Driscoll et al. 2005). We used an information theoretic approach to assess the relative importance of seven *a priori* candidate models developed based on factors proposed to influence Wood Thrush nesting success.

METHODS

Study Sites.—We conducted field work in southwestern Pennsylvania during 2003 and 2004 at six parks (2–30 km apart) in northeastern Allegheny County near or in Pittsburgh (Table 1). Sites (11–24 ha) were within forest (>100 ha) in a landscape characterized by irregularly shaped forested areas interspersed with roads, houses, grassy recreational areas, and a few fields. All sites were in edge habitat, defined as forest <200 m from a hard edge (Driscoll 2001; F. L. Newell, unpubl. data). We defined these sites as fragmented forest because core forest area in the sur-

TABLE 1. Study sites across an urban to forested gradient in southwestern Pennsylvania, 2003–2004. Core forest area (>200 m from an edge) occurred only in the contiguous landscape. Landscape characteristics were measured within a 5-km radius of the study site.

	Urban		Suburban		Rural		Contiguous
Parameter	Schenley Park	Frick Park	Guyasuta Camp	North Park	Hartwood Acres	Deer Lakes Park	Powdermill Nature Reserve
Latitude/longitude	40° 26′ N 79° 56′ W	40° 26′ N 79° 54′ W	40° 30′ N 79° 55′ W	40° 37′ N 79° 48′ W	40° 35′ N 79° 54′ W	40° 37′ N 79° 48′ W	40° 09′ N 79° 16′ W
Forest, %	23	27	50	53	60	63	84
Urban, %	63	56	26	15	6	6	0
Agriculture, %	3	4	14	5	12	12	3

rounding landscape was negligible. We grouped fragmented forest sites as urban (>50% urban), suburban (10–50% urban), and rural (<10% urban). We use 'rural' to indicate non-urban rather than agricultural. One large 100-ha site was studied at Powdermill Nature Reserve in Westmoreland County, 75 km southeast of Pittsburgh in the western foothills of the Appalachian Mountains (Table 1). We defined this site as contiguous because it was on the edge of a large forest (>10,000 ha). Nests at Powdermill were found in both the forest interior and in edge habitat adjacent to a small housing development. Landscape metrics were calculated using the program ATtTILA 4.0 (Ebert and Wade 2003) and we used land cover in a 5-km radius as the strongest predictor of nest predation rates (Hartley and Hunter 1998).

All sites were second-growth forest reverting from agricultural land use. The topography was gentle slopes or ravines adjacent to streams. Mesic forest was characterized by a canopy of maple (*Acer* spp.), yellow poplar (*Liriodendron tulipfera*), American beech (*Fagus grandifolia*), and ash (*Fraxinus* spp.) with an understory of common spicebush (*Lindera benzoin*), witch hazel (*Hamamelis virginiana*), and other species. Ground cover included plant species such as poison ivy (*Toxicodendron radicans*), Pennsylvania smartweed (*Polygonum pensylvanicum*), Virginia knotweed (*P. virginianum*), clearweed (*Pilea pumila*), cleavers (*Galium tinctorium*), and white snakeroot (*Eupatoruim rugosum*) as well as invasive Garlic mustard (*Alliaria officinalis*). Species typical of northern hardwoods were present at Powdermill including eastern hemlock (*Tsuga canadensis*), black birch (*Betula lenta*), and yellow birch (*B. alleghaniensis*) with striped maple (*Acer pensylvanicum*) and green brier (*Smilax rotundifolia*) in the understory. The herbaceous vegetation was dominated by fern species.

Nest Monitoring.—We searched for Wood Thrush nests from mid-May through the end of July. We were unable to find all nests at each site, but we attempted to find a representative sample by focusing search efforts on probable territories and using song playback to locate males (especially at fragmented forest sites). Nests were found by both intensive searching and parental behavior cues. Contents of nests <6 m above ground level were checked using a convex mirror attached to an aluminum pole. If the nest was above this height, we observed parental behavior to indicate activity and, when possible, nesting stage. High nests were considered inactive if either fledglings were found or there was no activity at the nest for 30 min and during subsequent visits (Martin et al. 1997). Nests were checked on average every 3–4 days.

Daily survival estimates and percent nesting success were calculated following Mayfield (1975) using a midpoint assumption between visits for failed nests and the last active day for successful nests or nests with uncertain fate (Manolis et al. 2000, Hazler 2004). Standard errors were calculated following Johnson (1979). We defined successful nests as those that fledged one or more young. We found over half of the nests before day 6 of incubation and, based on our data, we used an average nesting cycle of 26 days. A few nest failures included in our data could have been due to causes other than predation (abandonment or weather). We used the midpoint date between when a nest was first found active and the last exposure day to examine seasonal changes in nesting success (Hazler 2004).

Habitat Measurements.—We measured habitat characteristics at each nest in August and September after the breeding season following Martin et al. (1997). We measured nest height (using a tape measure or clinometer), distance from the main stem, and diameter of the largest support branch (estimated for nests >3 m above ground). The nest substrate was identified to species. We qualitatively scored foliage cover (0–3 scale) within 1 m of the nest in the four cardinal directions as well as above and below the nest. We used an average of these scores as an indicator of the visibility of the nest. We used four ropes attached to tent stakes to establish quadrants of a circular study plot centered on the nest to measure microhabitat (Martin et al. 1997). We counted two sizes of woody stems (<2.5 and 2.5–8 cm) within a 5-m radius of the nest, and two tree classes (23–38 and >38 cm) within an 11.3-m radius of the nest. We measured percent canopy cover with a spherical densiometer (an average of four readings standing at the nest site) and canopy height for a typical canopy tree using a clinometer. Nest locations

TABLE 2. Candidate models to explain Wood Thrush nest success across an urban to forested gradient in southwestern Pennsylvania, 2003–2004. Nest placement provided the best model with the lowest ΔAIC_c value but understory around the nest provided an equally plausible model. Both models combined explained the majority of the data.

Model	k	AIC_c	Δ_i	ω_i	Variable(s)
Nest placement	4	587.61	0.00	0.64	nest height, distance to bole, support branch diameter
Understory	3	589.23	1.62	0.28	number of small stems, number of large stems
Season date	2	592.64	5.03	0.05	midpoint date for the nest exposure period
Edge effect	2	593.60	5.99	0.03	distance to the nearest road, mowed grass, or field
Canopy trees	5	598.75	11.15	0.00	canopy cover, canopy height, number of large trees, number of medium trees
Concealment	2	599.85	12.24	0.00	average score of foliage cover around the nest
Urbanization	2	601.26	13.65	0.00	% urban within a 5-km radius of the study site

were recorded using a Magellan GPS (accurate to ~10 m) and superimposed on GIS maps in Arcview to measure distance to the nearest forest edge; slight adjustments were made for mapping error.

Statistical Analyses.—Mayfield logistic regression was used to incorporate explanatory variables into our analysis of Wood Thrush nesting success; we reversed signs to model survival (Hazler 2004). Statistical analysis was conducted with program SAS 9.0 (SAS Institute, Cary, NC, USA). We selected the best model to describe the data using an information-theoretic approach (Burnham and Anderson 2002). We selected the most meaningful variable from an ecological perspective for highly correlated data (Spearman's $r \geq 0.70$) (variables dropped were % forest, % agriculture, % understory, plant DBH, and plant height). Other habitat variables (leaf litter depth, % ground vegetation, small trees, number of support branches, and distance to water) also appeared to have limited relevance to Wood Thrush nesting success and were excluded. All models were multiplied by a variance inflation factor (deviance) to adjust for over dispersion of data as nests at the same site may not be independent if they are in the territory of one nest predator or renests of the same parent (Hazler 2004). The best model was selected based on the lowest value for Akaike's Information Criterion corrected for small sample size (AIC_c). Subsequent models were assessed based on their difference from the best model (ΔAIC_c) while models with Δ_i <2 were considered equally well supported. We used Akaike's weights (ω_i) to examine the extent to which our evidence supported the model. Models with Δ_i <10 were considered to have no explanatory value (Burnham and Anderson 2002). We used program CONTRAST (Hines and Sauer 1989) to examine Mayfield nesting success; this program conducts a contingency Chi-square test between groups. We conducted Mann-Whitney *U*-tests using a standard normal approximation for large sample size to compare nest placement and nest site microhabitat characteristics between edge and interior nests. Means are reported ± SE.

RESULTS

We monitored 44 Wood Thrush nests in 2003 and 85 in 2004. Search effort remained constant, but familiar study sites and experience with the target species resulted in twice as many nests being found in 2004. Search effort was consistent between sites; thus, differences in the number of nests found were related to breeding density. Nests ranged in height from 1 to 19 m and spicebush was the most common nest substrate (28%), often with support of grapevine or green brier (36%). Overall Mayfield success was 40% in 2003 (0.965 ± 0.008) and 42% in 2004 (0.968 ± 0.005). Thus, we pooled data between years because of small sample size.

Nest placement, based on the lowest AIC_c for the explanatory variables that we tested, provided the best model but the number of understory stems provided an equally plausible model (Table 2). There was strong evi-

TABLE 3. Parameter estimates for the two top models describing Wood Thrush nest success in southwestern Pennsylvania, 2003–2004. Nest height was associated with nest success while number of small understory stems was associated with nest predation.

Model	Parameter	Estimate ± SE	*P* value
Nest placement	Intercept	2.647 ± 0.343	<0.05
	Nest height	0.177 ± 0.069	<0.05
	Distance to bole	0.222 ± 0.120	0.06
	Support branch diameter	−0.124 ± 0.091	0.17
Understory	Intercept	4.237 ± 0.295	<0.05
	Number of small stems	−0.011 ± 0.033	<0.05
	Number of large stems	−0.001 ± 0.013	0.93

dence favoring these two models ($\omega_i > 90$). Nest height was associated with nest success while the number of small understory stems was associated with predation (Table 3). The negative correlation between these variables ($r = -0.50$, $P < 0.05$) suggests the two top models were closely related. Successful nests averaged >1 m higher with about a third fewer small stems surrounding the nest compared to failed nests (Table 4). Mayfield success was 20% higher for nests above the median nest height of 3 m with 53% (0.976 ± 0.005) of high nests successfully fledging young compared to only 31% (0.956 ± 0.008) of low nests ($\chi^2 = 4.53$, df = 1, $P < 0.05$). There was limited support for models that included season date and distance to the forest edge. The midpoint for successful nests averaged about 6 days later (25 Jun ± 2 days vs. 19 Jun ± 3 days) than for failed nests. Successful nests averaged 163 ± 17 m from the forest edge while failed nests averaged 110 ± 14 m. There was no evidence that nest concealment, forest canopy trees, or percent urban in the surrounding landscape provided a valid model for Wood Thrush nest success.

We did not find any apparent increase in nesting success along an urban to forested gradient. The highest success occurred at the suburban sites, although this was likely confounded by small sample size and/or low breeding density (Table 5). Our Mayfield estimates in fragmented forest across all sites averaged 42% (0.967 ± 0.006). We were not able to examine edge effects in fragmented forest because all forests, although moderate in size, were fragmented by some type of hard edge, typically roads, mowed grass, or fields. We did find edge effects at one contiguous forest site and Mayfield success was twice as high for interior nests compared to edge nests adjacent to a small housing development ($\chi^2 = 5.36$, df = 1, $P < 0.05$) (Table 5). Excluding the two suburban sites, Mayfield success for nests in the forest interior was 20% higher than for edge nests in fragmented forests ($\chi^2 = 2.36$, df = 1, $P = 0.12$) (Table 5). Wood Thrush nests in the forest interior were placed

TABLE 4. Mean ± SE for Wood Thrush nest site characteristics and microhabitat around the nest in relation to nest fate, southwestern Pennsylvania, 2003–2004.

Variable	Successful *n* = 73	Failed *n* = 54
Nest height, m	4.6 ± 0.4	3.3 ± 0.3
Distance to bole, m	1.5 ± 0.2	1.1 ± 0.2
Support branch diameter, cm	1.5 ± 0.1	1.8 ± 0.2
Concealment score, 0–3	1.6 ± 0.1	1.4 ± 0.1
Number of small stems, <2.5 cm	60.5 ± 4.8	89.6 ± 6.2
Number of large stems, 2.5–8 cm	12.3 ± 1.1	14.9 ± 1.5
Canopy cover, %	85.1 ± 1.7	80.4 ± 2.2
Canopy height, m	28.6 ± 0.6	26.9 ± 0.8
Number of medium trees, 23–38 cm	2.9 ± 0.2	3.3 ± 0.3
Number of large trees, >38 cm	2.4 ± 0.2	2.0 ± 0.2

TABLE 5. Mayfield nesting success for Wood Thrushes across an urban to forest gradient in southwestern Pennsylvania, 2003–2004. Wood Thrushes were half as successful in edge habitat compared to the interior of contiguous forest. Small samples of nests at urban and suburban sites were related to breeding density while the few nests monitored at suburban sites were quite successful.

Parameter	Edge habitat (<200 m)				Interior
	Urban	Suburban	Rural	Contiguous	
Daily survival ± SE	0.963 ± 0.018	0.985 ± 0.009	0.961 ± 0.009	0.948 ± 0.012	0.981 ± 0.006
Mayfield success (nests)	38% (9)	67% (15)	36% (39)	25% (33)	60% (31)
Observation days	109	198	490	367	461

almost 2 m higher in a third less understory (mean height = 5.4 ± 0.8 m, mean number of small stems = 54.6 ± 8.7) compared to all edge nests at both contiguous (mean height = 3.7 ± 0.3 m, mean number of small stems = 77.0 ± 7.5) and fragmented forest sites (mean height = 3.5 ± 0.3 m, mean number of small stems = 79.7 ± 5.4) (height: $z = 2.18$, $P < 0.05$; small stems: $z = -2.59$, $P < 0.05$).

DISCUSSION

Our results indicate that nest placement and/or microhabitat around the nest can be associated with Wood Thrush success. Model selection suggested that low Wood Thrush nests in dense understory may be especially vulnerable to predators. Artman and Downhower (2003) also found low nest height and dense understory associated with predation of Wood Thrush nests. Understory nesting species generally appear to experience the highest levels of nest predation (Martin 1993) while failed nests tend to average lower in height than successful nests (Best and Stauffer 1980, Wilson and Cooper 1998, Schmidt and Whelan 1999, Borgmann and Rodewald 2004). Other studies have found no association between nest height and success (Filliater et al. 1994, Hoover and Brittingham 1998, Rodewald and Yahner 2001). Low average nest height (~2 m) may provide an insufficient range to identify any effects or there may be interspecific differences in nest predation, perhaps associated with body size. However, different predator communities most likely are involved in the contradictory results between studies.

The best model from our data described the accessibility of nests to ground foraging mammalian or snake predators (i.e., higher nests placed farther out on small branches would be more difficult to access by climbing). Our study focused predominantly on edge habitat and changes in the nest predator community associated with forest fragmentation are a possible reason for the differences observed. Increased predation by common raccoons (*Procyon lotor*) may occur along suburban forest edges (Danielson et al. 1997) and raccoons, along with their tracks, were repeatedly observed at our study sites. Predation of low nests has often been ascribed to mid-level ground foraging mammals (Best and Stauffer

1980, Schmidt and Whelan 1999, Borgmann and Rodewald 2004). Schmidt (2003) showed that low nesting species in Illinois, vulnerable to predation by raccoons, have generally experienced population declines while video monitoring of natural forest nests found highest predation by raccoons in forest habitats (Thompson and Burhans 2003). However, other avian and snake predators observed at our study sites can increase along forest edges (Chalfoun et al. 2002a). Both black rat snakes (*Elaphe obsoleta*) and American Crows (*Corvus brachyrhnchos*) have been documented as predators of Wood Thrush nests (Farnsworth and Simons 2000). We do not know the specific nest predators, but the predator community likely influenced the effects of nest placement on nesting success in our study.

We did not find any support for our concealment model. The negative relationship between number of small stems and nest success suggests that understory did not provide concealment. This could be related to the predator community and whether predators are visually oriented (Johnson 1997) creating trade-offs between concealment and a view of the surroundings (Göttmark et al. 1995). Weidinger (2002) found that nest defense was more important than concealment for species such as the Wood Thrush that build large obvious nests. Aggressive nest defense has been observed while checking Wood Thrush nests (R. R. Roth, pers. comm.; F. L. Newell, pers. obs.) and real Wood Thrush nests have higher success than artificial nests suggesting that nest defense may improve success (Wilson et al. 1998). Male nest attendance as an indicator of defense was associated with Wood Thrush success when Blue Jays (*Cynocitta cristata*) were the main nest predator (Schmidt and Whelan 2005). Accessibility to predators and nest defense are not necessarily exclusive, and higher nest placement midway on the branch over an open area may make the nest less accessible, as well as allowing the bird to attack a predator (Wilson and Cooper 1998).

Selecting nest sites that limit predation has been proposed as a possible mechanism driving the evolution of species-specific nest placement in birds (Martin 1988, 1998). We found that nest placement was associated with success in our study, but were not able to directly ascertain if this influenced nest-site selection. Wood Thrush nest height can vary extensively and although most nests are below 6 m, some can be as high as 20 m (Roth et al. 1996; F. L. Newell, pers. obs.). Average nest height also varies as much as 3 m between studies (Roth et al. 1996, Hoover and Brittingham 1998, Artman and Downhower 2003, Powell et al. 2005). Presumably, these differences are associated with habitat structure (James et al. 1984), although possible bias associated with nest searching methods should be considered (Rodewald 2004, Powell et al. 2005). Wood Thrushes in our study tended to nest lower in a thick shrub layer in edge habitat. Correlations between nest height and understory suggest the availability of low nest sites may influence site selection if shrubs provide the branch architecture for low nest placement in the forest (Schmidt and Whelan 1999, Borgmann and Rodewald 2004). Wood Thrushes preferentially select nest sites with a higher density of shrubs than randomly available (Hughes 1977, Hoover and Brittingham 1998, Artman and Downhower 2003). If Wood Thrushes have evolved to select nest sites with dense foliage, this could encourage low nest placement in edge habitat, in part creating an ecological trap (Gates and Gysel 1978) which could exacerbate predation along the forest edge. Low nest height and accessibility to predators have been proposed as the mechanism leading to increased nest predation in exotic shrubs (Schmidt and Whelan 1999, Borgmann and Rodewald 2004).

Edge was not an important model for nest predation in our study. We found a significant edge effect at one contiguous forest site, unlike Driscoll and Donovan (2004), perhaps because of close proximity to a housing development (Phillips et al. 2005). We predominantly monitored Wood Thrush nests in edge habitat and any effect that continued 200 m into the forest would be difficult to identify. Mayfield success across fragmented forest sites of 42% is comparable to studies in large forests (Donovan et al. 1995, Farnsworth and Simons 1999, Driscoll and Donovan 2004). Nesting success may be density dependent (Martin 1988, Sillett et al. 2004) and results at urban and suburban sites could be related to low breeding density (≤3 males singing except for North Park in 2004). Our data were also confounded by small sample sizes because of low breeding density. Thus, our results are inconclusive. Other research has found that urbanization may not be associated with increased nest predation although additional factors influence population dynamics in urban areas (Rodewald and Shustack 2008).

Differences in success related to nest height and understory in our study occurred across a range of locations suggesting the results were not site specific. We were not able to identify the underlying causal mechanism(s) for these results. Survival of natural nests reflects effects of both nest placement and/or nest defense (Weidinger 2002). Our results suggest several non-exclusive explanations: (1) changes in understory density could encourage Wood Thrushes to nest lower making their nests more vulnerable to predators and/or limiting nest defense, and (2) changes in the predator community could make low nests more vulnerable in edge habitat. A moderate midstory, 3–6 m in height, with saplings and small trees probably provides the most suitable nesting habitat for Wood Thrushes (R. R. Roth, pers. comm.). The possibility that management to limit dense understory would benefit Wood Thrush nesting success should be studied further. Study of specific predators and their foraging behavior in edge habitat may explain the association between nest placement and success in our study.

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EFFECTS OF EXPERIMENTAL EGG COMPOSITION ON REJECTION BY VILLAGE WEAVERS (*PLOCEUS CUCULLATUS*)

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ABSTRACT.—We experimentally parasitized nests of the Village Weaver (*Ploceus cucullatus*) in Hispaniola using real and artificial eggs made from wood and modeling clay. Artificial eggs were similar in size and shape to real weaver eggs and were coated with acrylic paint and glazed. Real eggs were actual weaver eggs taken from Village Weaver nests. Experimental parasitic eggs (1) mimicked natural weaver eggs, (2) differed in color only, (3) differed in spotting only, or (4) mimicked Shiny Cowbird (*Molothrus bonariensis*) egg color and spotting pattern. Parasitized nests were checked after 2–6 days. Real eggs were ejected from weaver nests with increasing frequency as they became less similar to the eggs in the nest with cowbirds eggs having the highest rejection (81%). However, for artificial egg types there were no significant within-composition differences in patterns of rejection. Clay eggs were usually ejected from the nests, whereas nests containing wood eggs often ended empty, or with only the artificial egg remaining in the nest. These patterns may reflect the differential ability of weavers to recognize and remove foreign eggs of different compositions from their nests. Researchers undertaking egg-rejection experiments should use real eggs either in addition or in place of artificial eggs to assess the cost of rejection and the coevolutionary relationships between parasite and host. *Received 8 September 2006. Accepted 17 January 2007.*

It is advantageous for individual birds to be able to recognize their own eggs and to remove foreign eggs from their nests when exposed to brood parasitism (Davies and Brooke 1989, Rothstein 1990, Ortega 1998, Peer et al. 2005). Addition of experimental eggs to nests of Old World cuckoo (*Cuculus* and *Chrysococcyx*) hosts and New World cowbird (*Molothrus*) hosts are often used to assess levels of egg rejection in avian populations (Rothstein 1975, Alvarez et al. 1976, Ortega and Cruz 1988, Davies and Brooke 1989, Lotem et al. 1995, Nakamura et al. 1998). Artificial eggs are used more often than real eggs because they are easily acquired and provide larger sample sizes (Rothstein 1970, Davies and Brooke 1989, Briskie 2003). Early studies used eggs formed of plaster of paris (Rothstein 1975), wood (Alvarez et al. 1976, Wiley 1982), wood putty (Cruz and Wiley 1989), gel-coat resin (Davies and Brooke 1989), and plastic filled with water (Ortega and Cruz 1988). More recently, eggs of solid plastic (Higuchi 1989, 1998; Moskát and Fuisz 1999) or modeling clay (Soler et al. 1995, Briskie 2003, Lee et al. 2005) have also been used. Real eggs have been used in relatively few studies (Jackson 1998, Lahti and Lahti 2002, Prochaska and Honza 2003, Antonov et al. 2006, Lahti 2006). Studies using both real and artificial eggs are relatively rare, with most focusing on cuckoo hosts (Lotem et al. 1995, Nakamura et al. 1998, Martin-Vivaldi et al. 2002) and a few (Rothstein 1976, 1977; Ortega and Cruz 1988; Cruz and Wiley 1989) on cowbird hosts. Thus, the results of many studies using artificial eggs cannot be supported with data on rates of egg rejection of real eggs.

Rothstein (1982a, 1982b) found that important components in the recognition process differed among species and included size, color, and pattern. Typically the size, shape, and color of artificial eggs can closely mimic that of real eggs, and some studies have also attempted to use artificial eggs that match the weight (Rothstein 1974, Alvarez et al. 1976, Moksnes et al. 1991) and thermal properties (Moskát and Fuisz 1999) of real eggs.

Besides differing in their ability to recognize foreign eggs, species differ in how they handle parasitic eggs. Types of rejection behavior include burial of the egg in the lining of the nest, crushing or piercing the egg, and

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egg-ejection either by grasping and dropping the whole egg from the nest, or by puncturing to more easily remove it (Rohwer and Spaw 1988, Ortega 1998, Peer et al. 2005). The type of rejection could strongly affect the host's ability to handle artificial eggs of different composition. Species that typically puncture-eject eggs may be unable to handle solid eggs of plaster, wood, or plastic. Alternatively, species with a small gape could have difficulty grasping and removing hard eggs from the nest (Rothstein 1977; Spaw and Rohwer 1987; Moksnes et al. 1991, 1994; Martin-Vivaldi et al. 2002). Use of "hard" artificial eggs may underestimate the frequency of rejection of natural parasitism and overestimate the cost of egg rejection by hosts (Martin-Vivaldi et al. 2002).

The Village Weaver (*Ploceus cucullatus*) is a common, colonially nesting species with highly variable egg color and spotting pattern (Collias 1984, 1993; Cruz and Wiley 1989). Village Weaver nests in Africa are parasitized by the Diederik Cuckoo (*Chrysococcyx caprius*), which also shows a wide range in egg coloration and pattern. Because of this selective pressure, Village Weaver females recognize and puncture-reject eggs that do not closely mimic their own (Reed 1968, Collias 1984, Lahti and Lahti 2002, Lahti 2005). Conspecific brood parasitism occurs at low rates in Village Weaver populations and does not appear to be a factor in development of egg rejection behavior (Victoria 1972, Collias 1984, Cruz and Wiley 1989, Lahti 2006). The Village Weaver was introduced into Hispaniola in the 1970s. Cruz and Wiley (1989) found that introduced populations in the Santo Domingo region had a lower rate of rejection of foreign eggs than African populations. However, the parasitic Shiny Cowbird (*Molothrus bonariensis*) colonized Hispaniola in the 1970s and 1980s (Arendt and Vargas Mora 1984, Cruz and Wiley 1989), and recent studies have shown the weaver's egg-rejection behavior has increased since that time (Robert and Sorci 1999). Lahti (2005, 2006), however, suggested there has been no significant decline in the Village Weaver's ability to recognize foreign eggs in the introduced population, but that egg rejection behavior had been compromised by decreased population variation in egg appearance and increased within clutch variability.

TABLE 1. Numbers and locations of Village Weaver colonies and nests on which egg-rejection experiments were undertaken in northwestern and central Dominican Republic, 1999–2001.

Nearest city	Colony name	Nests parasitized	Nests with data
Monte Cristi	Kilometer 14	48	46
	Kilometer 34	11	10
	Kilometer 35	32	31
	Alex y Pablo	14	06
	The Canal	09	09
	La Bega	55	46
	Los Duros	40	36
Bonao	Finca Cabral	107	92
	Lopez	10	05
	Señora Cruz	49	46
San Francisco	Kilometer 13	94	87
	Basily	20	19
	Villa Tapia	10	10
Totals	13	499	443

We experimentally parasitized nests using mimetic and non-mimetic real and artificial weaver eggs, and Shiny Cowbird egg mimics (henceforth cowbird eggs) as part of a study of egg rejection behavior in the Village Weaver, a puncture-ejecting species, in Hispaniola. We compared Village Weaver response to real and artificial eggs of different materials (modeling clay and wood). We predicted that: (1) rejection or acceptance of mimetic and non-mimetic weaver and cowbird eggs by weavers was independent of type of egg used in experimental parasitism, and (2) weavers would accept mimetic weaver eggs but would reject non-mimetic weaver and cowbird eggs.

METHODS

Study Sites.—We experimentally parasitized weaver nests from 1999 to 2001 at 13 colonies in the northwestern (Monte Cristi) and central (Bonao and San Francisco de Macoris) regions of the Dominican Republic (Table 1). Weaver colonies were typically in large trees in cattle pastures and around the edges of agricultural fields, especially rice.

Egg Experiments.—Artificial eggs were similar in size and shape to real eggs and were made of wood or plasticine modeling clay (henceforth clay) coated with acrylic paint and a clear glaze, resulting in artificial eggs that mimicked real eggs. The wood eggs were made on a lathe and the clay eggs were hand sculpted. Artificial weaver eggs were painted shades of light blue, green, or blue-green within the range of variation for real Hispaniolan weaver eggs. We compared artificial eggs with real weaver eggs in the field to assure resemblance to real eggs prior to use. We painted artificial cowbird eggs off-white typical of Shiny Cowbird eggs. All artificial cowbird eggs and about half of the artificial weaver eggs were spotted or blotched with dark brown or blackish-brown. Spotting varied in intensity on different eggs but was within the range exhibited by real weaver and cowbird eggs. Cowbirds eggs were the most divergent in appearance from weaver eggs.

Artificial eggs varied in size, but were within the range of variation exhibited by real weaver and cowbird eggs. Wood eggs ranged from 15.3 to 15.7 mm in width (mean ± SD, 15.5 ± 0.2 mm, n = 21) and from 21.3 to 21.9 mm in length (mean 21.6 ± 0.2 mm, n = 21), whereas clay eggs ranged from 14.5 to 16.3 mm in width (mean 15.5 ± 0.2 mm, n = 21) and from 21.0 to 22.1 mm in length (mean 21.5 ± 0.2 mm, n = 21). Real weaver eggs ranged from 14.2 to 16.8 mm in width (mean 15.2 ± 0.9 mm, n = 85) and from 19.8 to 26.3 mm in length (mean 22.3 ± 1.1 mm, n = 87). Real Shiny Cowbird eggs from a previous study measured 16.5 ± 0.6 mm in width and 20.7 ± 0.9 mm in length, n = 235 (Cruz and Wiley 1989).

Egg masses were within the range of variation exhibited by real weaver and cowbird eggs. Real weaver eggs ranged from 1.7 to 3.4 g (mean 2.6 ± 0.5 g, n = 25, [Din 1992]) and cowbird eggs ranged from 2.5 to 3.5 g (mean 3.0 ± 0.3 g, n = 9, [Manolis 1982]). Wood eggs ranged from 1.7 to 2.1 g (mean 1.96 ± 0.1 g, n = 21) and clay eggs ranged from 2.6 to 3.4 g (mean 3.1 ± 0.2 g, n = 21).

Real eggs used in the experimental parasitism were viable Village Weaver eggs taken from active nests. Cowbird eggs were not readily available; we used real weaver eggs painted off-white and speckled with dark brown or blackish-brown, and glazed to match the color and spotting of cowbird eggs. The choice of foreign egg to be used in each trial was assigned using randomly generated tables. Experimental eggs were of four classes: (1) mimetic - eggs resembling real eggs in a nest in both color and spotting pattern; (2) different ground color - eggs similar in spotting to the real eggs, but differing in ground color; (3) different spotting - eggs similar in ground color to real eggs but either spotted or unspotted to differentiate them from real eggs; and (4) weaver eggs painted to resemble cowbird eggs. We also used some nests (n = 24) as "control" nests. The eggs in these nests were manipulated in the same way as eggs from experimental nests, but all of the original eggs were returned to the nest and no foreign eggs were added.

We checked all nests on each visit to a colony that were accessible from the ground or from ladders placed against the colony tree. We did not check nests more frequently than every 2–6 days to minimize disturbance at the colonies. Egg-rejection by Village Weavers normally occurs within 24 hrs of parasitism (Victoria 1972, Cruz and Wiley 1989). We ascertained nest contents by reaching through the entrance hole and gently feeling the interior. We removed the eggs from each nest and recorded their number, color, and spotting pattern. We marked each nest using a small numbered piece of tape on a twig adjacent to the nest. In nests that contained only one egg, the egg was returned to the nest and a foreign egg was added. In nests that contained more than one egg, one of the real eggs was removed for use in other experimental parasitism, and the remaining eggs were returned to the nest along with a foreign egg. Real eggs used in experimental parasitism experiments were marked with a small dot on the tip using an indelible ink marker so they could be differentiated from other eggs in the nest. The eggs were removed in control nests and one was marked as described above. All eggs were then returned to the nest. On return trips to the same colony, new nests with eggs were experimentally parasitized, and previously parasitized nests were checked and their contents recorded.

No nest was used more than once. We could not be absolutely certain we were not parasitizing nests of the same female weaver over time as weavers might have renested within the same colony, or moved among colonies. However, our methods should have minimized potential psuedoreplication (Hurlbert 1984)

TABLE 2. Artificial parasitism experiments on Village Weaver nests using real and artificial eggs, northwestern and central Dominican Republic, 1999–2001.

	n	Egg accepted	Egg rejected	Parasitic egg rejected	Nest empty
Real egg					
Control	24	91.7%	0	0	8.3%
Mimetic	77	72.7%	18.2%	0	9.1%
Different ground color	38	63.2%	31.6%	0	5.3%
Different spotting	52	32.7%	61.5%	0	5.8%
Cowbird	36	2.8%	80.6%	0	16.7%
Wood egg					
Mimetic	32	21.9%	31.2%	25.0%	21.9%
Different ground color	23	17.4%	17.4%	26.1%	39.1%
Different spotting	33	30.3%	21.2%	15.2%	33.3%
Cowbird	53	15.1%	34.0%	22.6%	28.3%
Clay egg					
Mimetic	19	0	94.7%	0	5.3%
Different ground color	13	0	92.3%	0	7.7%
Different spotting	20	5.0%	80.0%	0	15.0%
Cowbird	23	0	91.3%	0	8.7%

because: (1) we parasitized nests in 13 different colonies in three separate regions of the Dominican Republic (Table 1), and (2) we visited each colony for a relatively short period of time (1–3 weeks) during which substantial renesting was unlikely.

Analyses.—We did not include data from any nest for which we could not find the marker flag to prevent erroneously identifying a nest. We included results from all other nests that contained unhatched eggs at different stages. We minimized the number of nests that would have been parasitized late in the incubation stage by visiting the colonies regularly. Egg-rejection rates have been shown to differ for some species between stages of the nesting cycle (Rothstein 1975, Lawes and Kirkman 1996, Welbergen et al. 2001) and we did a pre-analysis test to examine if this was the case in our study. There was no difference in rejection of eggs from nests that were parasitized during egg-laying (25.0%, $n = 12$) and those parasitized during incubation (17.2%, $n = 58$) ($\chi^2 = 0.37$, $P = 0.54$, df = 1). We used Chi-square goodness of fit tests for all contingency tables.

RESULTS

We parasitized 499 nests in 13 colonies of which 443 nests produced useable data (Table 1). We observed large differences in the results of our experimental parasitism depending on type of egg used in the experiment. Overall, about 9% of nests ended empty (Table 2). There were significant between-pattern differences in results of the experiments using real eggs ($\chi^2 = 73.09$, $P < 0.0001$, df = 6). The proportion of introduced real eggs rejected by weavers increased as those eggs became less similar to the others in the nest (Table 2). There were no between-pattern differences ($\chi^2 = 5.19$, $P = 0.16$, df = 3) in the proportion of nests ending empty although the proportion was highest for nests parasitized with "cowbird" eggs (Table 2). Eggs were not rejected from control nests, but two of 24 (8.3%) ended empty after manipulation (Table 2).

Real mimetic eggs were less likely to be rejected than real eggs that differed in spotting pattern from those in the nest ($\chi^2 = 24.66$, $P < 0.0001$, df = 1). Mimetic eggs were also less likely to be rejected than cowbird eggs ($\chi^2 = 66.71$, $P < 0.0001$, df = 1). Rejection rates of mimetic eggs, however, did not differ from eggs that differed in color from those in the nest ($\chi^2 = 2.75$, $P = 0.09$, df = 1). Eggs with different spotting pattern from those in the nest were significantly more likely to be rejected than those that differed in ground color from other eggs in the nest ($\chi^2 = 6.52$, $P = 0.01$, df = 1). Cowbird eggs were more likely to be rejected than real eggs that differed in spotting pattern ($\chi^2 = 13.69$, $P = 0.0002$, df = 1) or color ($\chi^2 = 31.85$, $P < 0.0001$, df = 1) from those in the nest.

Nests in which artificial eggs were introduced had different patterns of acceptance and rejection from experiments using real eggs. Our null hypothesis that rejection or acceptance of mimetic and non-mimetic weaver eggs and cowbird egg types was independent of type of egg used in experimental parasitism is rejected. Furthermore, the pattern differed between wood and clay eggs. Wood eggs were accepted 20.5% of the time and rejected 27.7% of the time (Table 2). The remaining nests either ended empty (29.8%) or with only the foreign egg remaining in the nest (22.0%). Only one clay egg (1.3%) was accepted in a weaver nest with almost 90% being rejected and about 9% of nests ending empty (Table 2). Clay eggs did not end alone in a nest. There were no between-pattern differences in the results of the experiments using wood ($\chi^2 = 5.70$, $P = 0.46$, df = 6) or clay eggs ($\chi^2 = 3.96$, $P = 0.68$, df = 4).

There were differences in the proportion of nests ending empty based on composition of the egg used in the parasitism experiment ($\chi^2 = 50.00$, $P < 0.0001$, df = 3). Nests containing wood eggs were more likely to end empty than nests containing other egg types ($\chi^2 = 49.78$, $P < 0.0001$, df = 1). There were no differences ($\chi^2 = 0.23$, $P = 0.89$, df = 2) in the proportion of nests that ended empty among control nests and those parasitized using real or clay eggs.

Patterns of egg-rejection differed ($\chi^2 = 107.44$, $P < 0.0001$, df = 2) between nests parasitized using wood eggs and those parasitized using clay eggs. Patterns of egg-rejection also differed between nests parasitized using real eggs and those using other egg materials. Egg-rejection rates were affected by egg color and pattern when real eggs were used, but not when artificial eggs were used. We did not undertake the statistical tests necessary for all comparisons as it was obvious that patterns of egg-rejection differed dramatically when real eggs were used versus eggs of other composition (Table 2).

DISCUSSION

Our study demonstrated that experimental egg composition can affect the results of an egg rejection study. Both the ability of Village Weavers to recognize foreign eggs and their ability to remove them from their nests appeared to have a role in the observed differences.

Data from our control group of nests, as well as from nests in which real and clay eggs were used, suggest the "natural" rate at which nests end empty is about 10%. This could have been due to nest abandonment caused by disturbance at the nest site, eggs being damaged during manipulation, or nest predation. Nests parasitized with wood eggs were more likely to end empty (Table 2). This may be explained by inability of weavers to remove wood eggs by puncture-ejection. Village Weavers typically remove foreign eggs by first "spiking" them to create a hole and then carrying them from the nest (Victoria 1972). The proportion of nests that ended empty for both wood eggs and other egg types was independent of color pattern of the artificial eggs. Thus, we believe the pattern of empty nests was not related to type, coloration, or spotting pattern of eggs used in the experiments.

The results of our trials using real eggs suggest that differences in color and spotting pattern allowed Hispaniolan Village Weavers to discriminate between their own eggs and foreign eggs with rejection rates of foreign eggs increasing as the egg became dissimilar from those in the nest. It appears that spotting pattern is the more important factor because foreign eggs differing in spotting pattern were rejected significantly more often than were foreign eggs differing in color. Spotting pattern increases the complexity of the appearance of the egg, which should aid in egg recognition and discrimination (Lahti 2006). Eggs differing in color, however, were not more likely to be rejected than mimetic eggs. Weavers that produce eggs that differ from conspecifics only in ground color (light blue vs. blue-green) may be harder to differentiate.

We believe the results of these experiments using real eggs are more representative of the pattern of egg-rejection for naturally parasitized nests of Hispaniolan weavers. The high rejection rates for cowbird eggs likely arise from being different from weaver eggs in color (white vs. blue or green) and spotting pattern. In addition, despite the presence of cowbirds at several of our sites, we did not find any parasitized nests. This suggests that actual parasitism may be hard to detect because cowbird eggs may be rejected quickly.

The rejection rates of artificial eggs of different composition may be explained by the ability of weavers to recognize and remove them from their nests. It appears that weavers had trouble removing wood eggs because nearly 30% of nests ended empty, a far higher rate than for any other composition (Table 2). In addition, nests containing wood eggs often ended empty except for the foreign egg (Table 2), a pattern that did not occur with other egg composition. Finally, acceptance of wood eggs was independent of egg pattern and was higher than expected for some color patterns (e.g., cowbird eggs). This suggests that some weavers may have accepted wood eggs because they were unable to remove them from their nest. A different pattern of rejection occurred when nests were parasitized with eggs made of clay. The rejection rate of these eggs was nearly 100% and was independent of egg pattern (Table 2), suggesting that weavers were able to recognize them as foreign and ejected them from their nests. We found many clay eggs thoroughly pecked, and/or smashed on the ground underneath the colonies. These eggs may have been easy to handle and eject from the nest as the weavers only needed to break the thin glaze to pierce a clay egg. The rejection patterns for both wood and clay eggs were dramatically different from the pattern we detected when using real eggs. The results of our study would have been dramatically different if only artificial eggs were used in the experiments.

Robert and Sorci (1999), in a previous study of egg rejection by Hispaniolan weavers, used artificial eggs made of plaster of paris to examine rejection rates of foreign eggs in weaver nests. They experimentally parasitized 83 nests and obtained rejection data from 58. They did not report how many nests ended empty in their study, and they treated deserted nests, or nests in which only the artificial eggs were present, as rejections. The latter assumption probably did not affect their study since most of these cases would probably be representative of actual egg-rejection attempts, during which real eggs were broken while attempting to remove the foreign eggs. They reported finding many of the artificial eggs broken under the nest trees suggesting weavers were generally able to crack and remove eggs made from plaster. The overall results of their study were broadly similar to ours with high rejection rates (89%) for cowbird-type eggs, low rejection rates (25%) for "mimetic" weaver eggs, and intermediate rejection rates (68%) for "non-mimetic" weaver eggs.

Cowbird parasitism is usually costly to hosts as accepter species typically raised fewer of their own offspring when parasitized (Chace et al. 2000, Peer et al. 2005). Village Weaver nests parasitized by Shiny Cowbirds produced fewer fledglings than unparasitized nests (Cruz and Wiley 1989). Additionally, there may be a cost in rejecting parasitic eggs; i.e., rejecter species may break their own eggs when trying to eject the parastic eggs (Davies et al. 1996, Lotem and Nakamura 1998, Røskaft and Moksnes 1998). However, artificial eggs do not mimic the resistance of parasitic eggs to breakage (Martin-Vivaldi et al. 2002), some being soft (e.g., clay eggs) and others hard (e.g., wood eggs). Rothstein (1977) found the rejection costs of real Brown-headed Cowbird (*Molothrus ater*) eggs by Baltimore Orioles (*Icterus galbula*) were less than ejection of artificial hard models. Real eggs were rejected whereas most artificial eggs, made from plaster, were damaged and left in the nest.

Martin-Vivaldi et al. (2002) found the cost of rejecting artificial eggs may not present a true picture of the rejection of real parasitic eggs by host species of European Cuckoo (*Cuculus canorus*). They examined costs to potential hosts when rejecting hard egg models to costs when rejecting real House Sparrow (*Passer domesticus*) eggs. Martin-Vivaldi et al. (2002) found, as noted by Antonov et al. (2006), House Sparrow eggs are less resistant to puncturing than cuckoo eggs, which may underestimate the costs of cuckoo parasitism. Real weaver eggs painted to resemble cowbird eggs may also be less resistant to puncture than Shiny Cowbird eggs (Spaw and Rohwer 1987, Picman 1989). However, as also noted by Martin-Vivaldi et al. (2002) for their study, we believe the data obtained using real eggs are more representative than those obtained by using artificial eggs.

We have several suggestions for researchers undertaking egg rejection experiments. First, we recommend using real eggs for egg-rejection experiments whenever possible and, ideally, real parasitic eggs, either in addition to, or rather than, artificial eggs (Røskaft and Moksnes 1998, Rothstein and Robinson 1998, Martin-Vivaldi et al. 2002, Antonov et al. 2006). In many cases, the actual rates of rejection of natural parasitism can only be measured by using real eggs in experiments (Rothstein 1976; Moksnes et al. 1991, 1994; Martin-Vivaldi et al. 2002; Antonov et al. 2006). Second, we suggest that when only artificial eggs are used, more than one type (one hard and one easy to handle) should be used as this combination may affect whether hosts accept eggs because they have no recognition or because they physically cannot handle a hard egg. Third, we suggest that a control sample of nests in which eggs are manipulated in the same fashion as experimental nests be used. This will allow researchers to obtain an estimate of how many nests end empty either because of natural predation or abandonment caused by manipulation of the nest rather than experimental parasitism. In our controls, we tested only for nest manipulation, removing and reintroducing the original eggs. We also recommend controls for the artificial eggs (Peer and Bollinger 1998). Finally, we suggest that researchers report the rate at which their nests end empty, and include these in analysis, rather than ignoring them or assuming this rate is affected only by predation.

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The Wilson Journal of Ornithology 119(9):711, 2007

WINTERING DISTRIBUTIONS AND MIGRATION OF SALTMARSH AND NELSON'S SHARP-TAILED SPARROWS: ERRATUM

JON S. GREENLAW[1,2] AND GLEN E. WOOLFENDEN[1,†]

Erratum

Table 2 in Greenlaw and Woolfenden (2007: 367) contains an error that was not corrected. The earliest arrival date of *Ammodramus nelsoni nelsoni* in South Carolina, based on specimens examined, should read 1 October and not 1 May. We apologize for this error.

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Greenlaw, J. S. and G. E. Woolfenden. 2007. Wintering distributions and migration of Saltmarsh and Nelson's Sharp-tailed sparrows. Wilson Journal of Ornithology 119:361–377.

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Short Communications

The Wilson Journal of Ornithology 119(4):712–716, 2007

Migration Timing of Canada Warblers Near the Northern Edge of Their Breeding Range

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ABSTRACT.—Canada Warblers (*Wilsonia canadensis*) are one of the last warblers to arrive in breeding areas in northern Alberta and one of the first to depart in autumn resulting in a condensed breeding chronology relative to other locally breeding wood warblers. Males arrived before females during spring migration, while in autumn, adult females departed prior to males. Second-year males arrived later (P = 0.029) than after-second year males. Adult males departed later (P = 0.015) than adult females. Hatch-year birds departed after adult females but prior to adult males. Female Canada Warblers remained in breeding areas for 62 days while males remained 72 days. These data provide the shortest documented breeding site occupancy estimate for any bird that shows a post-nuptial molt. The short time spent in breeding areas may impose energetic constraints that influence breeding, molt, and survival, particularly for females. *Received 21 August 2006. Accepted 7 March 2007.*

Migration timing can strongly influence fitness (McNamara et al. 1998) and imposes temporal constraints to completing annual activities including territory establishment, breeding, and molt. Individuals that arrive later likely have tighter time constraints in breeding activities compared to early arriving individuals. Time and energetic constraints are even more intense when populations are at the northern edge of their breeding distribution (Briskie 1995).

The Canada Warbler (*Wilsonia canadensis*) is one of the least studied warblers and information concerning its breeding ecology and population dynamics is mostly lacking (Conway 1999). The northern and most western breeding populations occur in north-central Alberta and eastern British Columbia (Semenchuck 1992, Conway 1999). Canada Warblers are among the latest warblers to arrive and earliest to depart (Conway 1999) potentially placing time constraints on breeding ecology (Forstmeier 2002, Smith and Moore 2005).

Male neotropical wood warblers generally arrive in breeding areas before females in spring while, within gender, after-second year (ASY) birds typically precede second-year (SY) birds (Francis and Cooke 1986, Morris and Glasgow 2001, Stewart et al. 2002, Smith and Moore 2005). Studies of timing of autumn migration for a variety of wood warblers have offered contrasting results for gender and age-class patterns. Some studies found that hatch-year birds (HY) departed earlier than after hatch-year birds (AHY) (Benson and Winker 2001, Andres et al. 2005, Benson et al. 2006), while others found no difference in age and gender migration patterns in autumn (Morris and Glasgow 2001).

When spring and autumn migration dates are known for breeding areas, it is feasible to estimate the duration the breeding range is occupied (Benson and Winker 2001). For example, Alder Flycatchers (*Empidonax alnorum*) were in breeding areas for 48 days in Alaska (Benson and Winker 2001) but for 72 days in southern Ontario (Hussell 1991). Therefore, northern populations have less time to complete breeding and molt activities than southern populations. Furthermore, individuals at higher latitudes often have lower survival than their southern counterparts and have increased investment in fewer reproductive attempts (Ardia 2005). The objectives of my study were to: (1) document arrival and departure dates for male and female Canada Warblers by age-class, and (2) provide estimates of breeding range occupancy on a study area close to the northern limit of the species range.

METHODS

Study Area and Field Methods.—Migration of Canada Warblers was monitored daily be-

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tween 1994 and 2005 by staff at the Lesser Slave Lake Bird Observatory (LSLBO) on the eastern shoreline of Lesser Slave Lake, Alberta (55° 20′ N, 114° 40′ W) as part of the Canadian Migration Monitoring Network (Dunn et al. 2006). Birds were captured within a 0.5-ha area of willows (*Salix* spp.) bordered by continuous aspen (*Populus tremuloides*) dominated mixed-wood boreal forest. Spring and autumn migration was monitored continuously in most years between 1 May and 10 June, and between 18 July and 30 September, respectively. Birds were captured using 12 nylon mist nets (30 mm, 3 × 12 m) from 30 min prior to sunrise to 6 hrs (1994–1999) or 7 hrs (2000–2005) thereafter. Net locations have been consistent since 1996, and were not greatly different in prior years.

Captured birds were banded, classified to age and gender by plumage attributes (Rappole 1983) and the extent of skull pneumaticization, and checked for breeding characteristics (Pyle 1997). Canada Warblers can be classified in spring as SY or ASY and autumn as HY or AHY. Occasionally individuals could not be reliably classified to age and gender for reasons such as the data not being recorded or intermediate plumage characteristics. Excluding unknown individuals from migration estimates could bias results if they are not a random sample of their gender and age class.

I used raw banding totals because banding effort occurred relatively uniformly throughout spring and autumn each year (Francis and Cooke 1986). Mean arrival and departure date varied between years, probably due to weather conditions, but I did not standardize capture dates to year because the effects of weather can influence both trapping efforts and population differences in migration timing. Data were pooled over the study period as sample sizes of some gender and age-classes were small.

I limited all records to original bandings (92% of all captures) to reduce bias of including birds using the site as a stopover over several days. I excluded birds in spring that were developing breeding characteristics (male: cloacal protuberance, female: brood patches) potentially indicating locally breeding individuals, and those captured after 9 June when most Canada Warbler captures shifted to previously banded individuals. I limited autumn records to captures after 19 July because prior to this date few Canada Warblers were captured, most captures were already banded, and new bandings likely represented dispersing individuals rather than true migrants (Carlisle et al. 2005). I included birds with breeding characteristics as they can be protracted in autumn migration. Birds that bred locally were likely already banded at adjacent MAPS (Monitoring Avian Productivity and Survivorship) sites during the breeding season.

Statistical Analysis.—I first ascertained if excluding records of unknown age or gender would bias arrival and departure date estimates of known groups using Wilcoxon tests. I only present these results where a difference was found. Kolmogorov-Smirnov two-sample tests were used for spring and autumn migration timing comparisons (Siegel and Castellan 1988, Carlisle et al. 2005). Dates for minimum estimates of breeding range occupancy were calculated by subtracting median arrival dates from median departure dates for adult males and females separately (Benson and Winker 2001). All statistical analyses were conducted with SPSS 13.0 (SPSS 2004) with significance at $\alpha = 0.05$.

RESULTS

Collectively, males arrived earlier than females in spring with ASY individuals arriving prior to SY's of both males and females (Fig. 1). Among males, the arrival date of ASY's was earlier ($D = 1.454$, $P = 0.029$) than the arrival date of SY's. ASY females arrived earlier than SY's, but this difference was not significant ($D = 1.143$, $P = 0.15$).

Males departed later in autumn than females (Fig. 2). A large proportion of autumn HY birds could not be classified to gender and these birds departed earlier than HY males and females ($Z = -6.411$, $P < 0.001$; Fig. 2). There was no difference between classified males and females in autumn departure dates for HY's ($D = 0.879$, $P = 0.42$), but this should be inferred cautiously because unknown HY's preceded males and females. AHY females departed first while AHY males departed last ($D = 1.569$, $P = 0.015$).

Overall, males arrived by 1 June and departed by 12 August, providing an indirect estimate of time spent in breeding areas of ap-

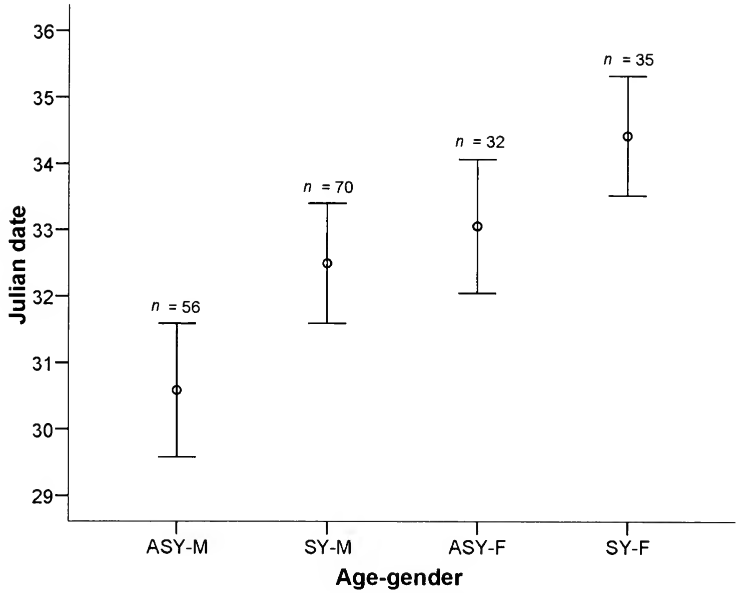

FIG. 1. Arrival of Canada Warblers in northern Alberta. Error bars represent mean and 95% CI of spring arrival date. Julian date 32 = 1 June.

proximately 72 days or 19.7% of the annual cycle. Females occupied breeding areas for approximately 62 days (17% of the annual cycle) arriving by 3 June and departing by 4 August.

DISCUSSION

Arrival and Departure.—Male Canada Warblers in northern Alberta arrived prior to females and older wood warblers arrived prior to younger individuals (Francis and Cooke 1986, Stewart et al. 2002) . Males may arrive earlier to acquire better breeding territories (Smith and Moore 2005) while females may arrive later to maximize survival as food is often less available in early spring (Nilsson 1994).

I found protogynous autumn migration in adult Canada Warblers with females departing prior to males. Other studies of wood warblers have reported either that males depart after females for MacGillivray's Warbler (*Oporornis tolmiei*) (Carlisle et al. 2005), Yellow-rumped Warbler (*Dendroica coronata*), and Magnolia Warbler (*D. magnolia*) (Mills 2005) or that females depart after males as for Wilson's Warbler (*Wilsonia pusilla*) (Carlisle et al. 2005). Later departure by males is thought to offer benefits in the following breeding season through exposure to and defense of potential breeding sites (Forstmeier 2002).

The patterns in departure of age classes of Canada Warblers in autumn are of interest because HY's were intermediate of adult (AHY) males and females. Contrasting migration strategies usually occur between neotropical migrants depending on timing of autumn molt. Carlisle et al. (2005) found strong correlation with molting strategy and migration timing of age-classes; AHY birds molting flight feathers near breeding areas departed later than HY individuals. Adult Canada Warblers have a post-nuptial (basic) molt and the expected pattern is for adults to leave after HY's. Males and females departed at different times and, thus, appear to have different strategies for autumn migration departure.

Indirect Estimate of Breeding Range Occupancy.—A measure of the time spent in breeding areas may indicate temporal constraints on reproduction timing, investment, and renesting ability. These parameters may be more critical for reproductive success at the northern limit of a breeding range compared to more southern locales. Occupancy of only 62 days for female and 72 days for male Canada Warblers in this study is shorter than documented for any other wood warbler, and is

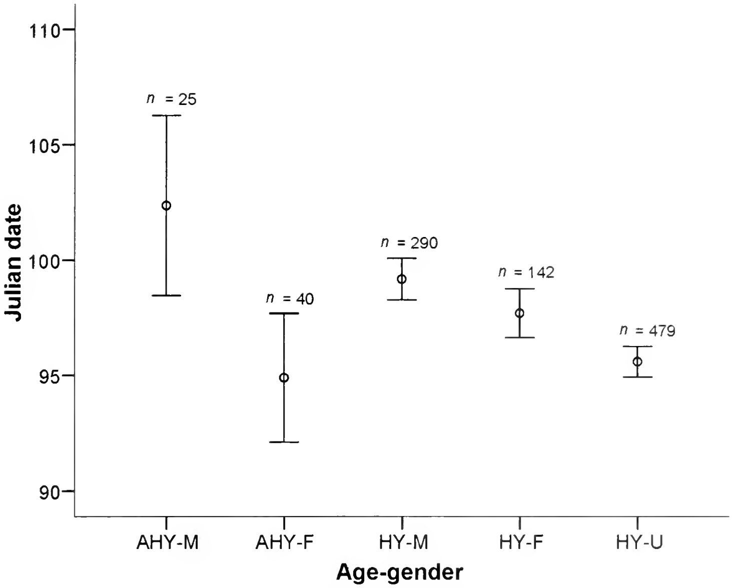

FIG. 2. Departure of Canada Warblers in northern Alberta. Error bars represent mean and 95% CI of autumn departure date. Julian date 93 = 1 August.

the shortest for any bird with a post-nuptial molt on or near breeding areas. Occupancy estimates for six species of wood warblers breeding in Alaska varied from 84 to 108 days (Benson and Winker 2001). Both late spring arrival and the need for early autumn migration offer the ability to test hypotheses concerning reproductive versus survival tradeoffs during temporally constrained periods in breeding areas that may ultimately influence conservation of the Canada Warbler. Future studies could investigate the implications of reduced occupancy time in breeding areas between northern and southern populations of Canada Warblers.

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Occurrence and Condition of Migrating Swainson's Thrushes in the British Virgin Islands

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ABSTRACT.—Swainson's Thrushes (*Catharus ustulatus*) migrate widely throughout North and Middle America. In the Caribbean, the species is known to occur only in the western-most Greater Antilles, and there only as a rare migrant. We captured and visually detected migrant Swainson's Thrushes beginning in 2000 at a banding station on Guana Island, British Virgin Islands. The majority of thrushes captured were adults (79%) and most had no (71%) or little fat (12%) reserves at time of capture; 61% were classified as being in emaciated or poor condition. The poor physiological conditions may have resulted from longer over water flights rather than island hopping. *Received 8 September 2006. Accepted 8 January 2007.*

The Swainson's Thrush (*Catharus ustulatus*) is a neotropical migrant passerine broadly distributed across the forested north and mountainous west of North America (Mack and Wang 2000). Population trends across the species' breeding distribution are inconsistent and difficult to interpret (Mack and Wang 2000), but there is evidence to suggest long-term declines in eastern North America (Holmes and Sherry 1988, Hill and Hagen 1991, Buckelew and Hall 1994). Recent analysis of Breeding Bird Survey (BBS) data indicates a declining trend (-0.83; $P = 0.09$) in the eastern United States (Sauer et al. 2005). Site-specific factors associated with breeding habitat may be influencing population trends (Sauer et al. 1997, Mack and Wang 2000), but population declines may also be related to factors occurring outside the breeding season (Petit et al. 1995, Mack and Wang 2000, Greenberg and Marra 2005). In particular, birds encounter a host of obstacles to survival during migration (Moore et al. 2005). The ecology of *en route* migrants is poorly understood (Heglund and Skagen 2005), which has been a major obstruction to progress on conservation of neotropical migrant birds (Cochran and Wikelski 2005).

An understanding of migration routes is nec-

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essary before assessing stopover habitat availability or distribution along migration routes. The known fall migration routes to wintering areas in southern Mexico, Central America, and northern South America differ between western and eastern populations of Swainson's Thrushes (Mack and Wang 2000). The eastern population appears to use different routes in autumn than in spring. The higher proportion of individuals on the eastern coast in autumn than spring may be indicative of more individuals making trans-gulf migrations during autumn, but circum-gulf migrations in spring (Child 1969, Rappole et al. 1979, Mack and Wang 2000, Reugg and Smith 2002). There also may be age-related differences in survival of Swainson's Thrushes migrating over open-water routes. Woodrey and Moore (1997) reported after-hatch-year (AHY) Swainson's Thrushes on the Alabama coast had sufficient energy stores to complete trans-gulf crossings, but hatch-year (HY) birds likely could not do so under still-air conditions.

The islands of the Caribbean have received little attention as a possible migration pathway for Swainson's Thrushes. The Swainson's Thrush within the Caribbean is considered a rare migrant in Cuba, Jamaica, the Cayman Islands, and northern Bahamas (Arendt 1992, Raffaele et al. 2003). This species was not listed in Raffaele's (1989) guide to birds of Puerto Rico and the Virgin Islands. Boal et al. (2006) reported capturing and banding the first Swainson's Thrushes reported for the Virgin Islands, approximately 1,300 km east of Jamaica. The objectives of this paper are to: (1) report the age and physical condition of autumn-migrating Swainson's Thrushes in the eastern Caribbean, and (2) examine the possible relevance of the increasing number of Swainson's Thrushes detected at our banding station.

METHODS

Our study site was on Guana Island (18° 30′ N, 64° 30′ W), immediately north of Tortola, the largest of the British Virgin Islands (BVI). The BVI, along with the U.S. Virgin Islands (USVI), are a chain of approximately 76 islands and cays. Guana Island is relatively small (3 km^2) compared to other inhabited islands such as Tortola (54 km^2) and Virgin Gorda (21 km^2). The British Virgin Islands have a subtropical climate tempered by northeasterly trade winds with temperatures ranging from 28 to 33° C and humidity levels ~78% throughout the year (Lazell 2005). The annual mean rainfall for Guana Island is estimated at 92 cm (Lazell 2005).

Guana Island is topographically rugged with elevations ranging from sea level to 246 m. Approximately 90% of the island is subtropical dry forest with mesic 'ghut' forests (5%) present in some drainages, and lesser amounts of human-altered areas (3%), mangroves (*Laguncularia* spp.) (1%), and beach (1%) (Lazell 1996). The primary native vegetation on Guana Island is tabebuia (*Tabebuia heterophylla*), gumbo-limbo (*Bursera simaruba*), loblolly (*Pisonia subcordata*), buttonwood (*Conocarpus erectus*), frangipani (*Plumeria alba*), acacia (*Acacia muricata*), and sea grape (*Coccoloba uvifera*). Tam-tam (*Leucaera leucocephela*) is common in disturbed areas. Introduced species include coconut (*Cocos nucifera*), tamarind (*Tamarinda indica*), and royal poinciana (*Delonix regia*) (Lazell 1996).

A banding station has been in operation on Guana Island each October from 1994 through 2006. Net locations were primarily along a northeast–southwest ridge and the southeast-facing slope of a mountain on the west side of the island. The majority of nets were in subtropical dry forest areas, but each year 2–3 nets were in human-altered areas along the ridge, all at approximately 70 m elevation. Duration of mist-netting operations and number of nets operated were subject to local meteorological conditions, an adequate number of individuals to assist with net monitoring, and the time we were allowed access to the island. Our nets were 12 m long with a mesh size of 32 mm; we typically monitored 12 nets, although the number was variable in earlier years of the banding station. Nets were opened at 0630 hrs and closed at 1100 hrs. However, nets were opened and operated during all daylight hours during migrant fallouts. We identified all birds captured to species and, when possible, gender and age (Raffaele 1989, Pyle 1997, Raffaele et al. 2003). We recorded wing chord and mass, estimated fat reserves, physiological condition, and banded each bird with an aluminum leg band provided by the U.S. Geological Survey, Bird Banding Laboratory. We measured mass with an electronic scale accurate to 0.1 g. Our fat estimates were based on the five categories presented by the North American Banding Council (2001). We used four categories to assess physiological condition of the breast muscle: emaciated, poor, fair, and good. Fat amounts and physiological condition were assessed by the same person for all but one thrush.

RESULTS

A Swainson's Thrush was first captured on Guana Island on 9 October 2000; we captured another and observed a second, unbanded individual on 16 October 2003. A fallout of Swainson's Thrushes occurred on Guana Island on 13 October 2005 and we captured 26 individuals between 13 and 15 October. Twenty-two (79%) of the 28 thrushes captured between 9 October 2000 and 15 October 2005 were AHY and 6 (21%) were HY birds. The average (±SD) mass of AHY birds (24.6 ± 2.2 g) was slightly lower than that of HY birds (26.4 ± 1.8 g). The difference approached statistical significance ($t_{26} = -1.85$, $P = 0.07$), but we suspect any difference may be related to a small sample of HY individuals. Seventeen (71%) of 24 thrushes examined had no fat reserves at time of capture, 4 (17%) had a trace of fat, 2 (8%) had a little fat built up, and 1 (4%) had a moderate amount of fat visible. We classified 1 (5%) thrush as emaciated, 12 (57%) as poor, 6 as fair (29%), and 2 (10%) of the 21 individuals as in good condition.

One AHY thrush captured at 1000 hrs on 13 October was recaptured at 0830 hrs on 14 October, 1400 hrs on 16 October, and 0650 hrs on 17 October. When originally captured, the thrush weighed 24.9 g, had no fat reserves, and was considered in poor condition. On 14 October the thrush weighed 26.0 g; it weighed 29.9 g on 16 October, and was evaluated as in fair condition with a moderate amount of fat visible. Thus it had gained 5.0 g in 3 days. It weighed 28.5 g on 17 October, possibly due to being captured before sunrise and, hence, after a nocturnal fast.

We did not conduct systematic surveys during the Swainson's Thrush fallout in October 2005 and estimates of the number arriving on Guana are subjective. We are confident that we captured only a small proportion of the Swainson's Thrushes in our immediate netting area during the fallout. We believe an estimate of 300 to 500 individuals in the area of our banding station is reasonable and probably conservative. A far greater number of Swainson's Thrushes likely made landfall on the island during the fallout.

DISCUSSION

Few studies of neotropical migrants have been undertaken in the eastern Caribbean (Wiley 2000). Ours is the only current and consistently operated autumn-migrant banding station east of Puerto Rico. This may explain our detection of previously unreported neotropical migrant species in the BVI, including Swainson's Thrush (Boal et al. 2006). The species is fairly cryptic and our observations may be evidence of a regular, if previously undocumented, migration route. However, during the fallout on Guana Island in 2005, we easily observed numerous individuals and groups moving about our study area; we doubt such a fallout would go unnoticed by ornithologists or experienced bird-watchers in the region.

If Swainson's Thrushes recently arrived in the east Caribbean, it may be due to anomalous weather events. The normal wind flow over the extreme southeastern United States and Gulf of Mexico in October is from northeast to southwest (Gauthreaux et al. 2005), resulting in crosswind displacement for which Swainson's Thrushes exhibit little or no compensation (Cochran and Kjos 1985). The storm track of most hurricanes and storms in the Caribbean would likely increase such a crossing wind. An east-to-west crossing wind would result in displacement to the west, and does not explain an approximate 1,300-km displacement east of the more commonly (yet still infrequently) used route over Jamaica (Raffaele et al. 2003).

Our data suggest at least some Swainson's Thrushes may use, or be shifting to use, the Atlantic Coast Migration Route identified by Lincoln (1935). Birds using this route "island-hop" through the Bahama Islands to the Dominican Republic, across the Greater Antilles, and south along the Lesser Antilles to South America (Lincoln 1935). Habitat loss has been identified as a possible force resulting in changes in some migration routes (Arendt 1992, Askins et al. 1992), and we may be witnessing early indications of a change in migration behavior of some Swainson's Thrushes. Alternatively, the poor condition and greater proportion of AHY thrushes arriving on Guana could be indicative of a longer open-water migration. Woodrey and Moore (1997) reported AHY Swainson's Thrushes had sufficient energy stores to complete a trans-gulf crossing, whereas HY birds likely could not under still-air conditions. Whether intentional or forced by weather conditions, fewer HY thrushes may have been able to survive if an extensive open-water crossing was undertaken. Additional data are needed on migration routes, specific stop-over site conditions, and habitats used by this species during migration before we can further speculate on associations between stop-over habitats and potential shifts in migratory routes.

Our observations have supplanted DeGraaf and Rappole's (1995) assertion that Swainson's Thrushes are absent from the Caribbean and expanded the ranges reported in Raffaele (1989), Arendt (1992), and Raffaele et al. (2003). Continued and increased monitoring effort for neotropical migrant bird presence and habitat use in the eastern Greater Antilles and the Lesser Antilles will be necessary to verify migration route use, changes in migration patterns, and development of an understanding of why such changes may be occurring.

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Daily and Seasonal Variation in Body Mass and Visible Fat in Mountain Chickadees and Juniper Titmice

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ABSTRACT.—Diurnal variations in body mass and visible fat scores were measured for seasonally acclimatized Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus ridgwayi*) to examine if they undergo winter fattening. Body mass varied with time of day and was highest in evening for both species in summer and winter. Body mass, expressed as percent mass increase from morning to evening, was 7.3% for summer chickadees, 7.6% for summer titmice, 9.1% for winter chickadees, and 6.1% for winter titmice. Body mass was not significantly higher in winter-acclimatized birds compared to summer-acclimatized birds. Visible fat scores were significantly elevated in winter-acclimatized Mountain Chickadees relative to summer. Mountain Chickadees and Juniper Titmice appear to have seasonally constant body mass rather than undergoing winter fattening. These data are similar to other North American species in the family Paridae but contrast with data on European parids. *Received 26 December 2006. Accepted 1 April 2007.*

Increased body mass and fat levels are a common pattern of many cold-temperate wintering passerines, enabling these birds to meet thermoregulatory demands and buffer against temporary foraging restrictions due to inclement weather (King 1972, Dawson and Marsh 1986, Swanson 1991, O'Connor 1995). Although fat reserves may lower the risk of starvation, they may also increase predation risk (Blem 1990, Witter and Cuthill 1993, Lilliendahl et al. 1996). Body mass and fat levels of tree-foraging birds typically change little seasonally compared with ground-foraging birds. This is associated with more predictable food supplies for tree-foraging birds than for ground-foraging birds (Rogers 1987, Rogers and Smith 1993).

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Lehikoinen (1987) presented four graphical models to illustrate the possible relationship between seasonal and daily variation in body mass. Two models appear most probable for small tree-foraging birds (Haftorn 1989). The first is the "constant morning weight strategy" and the second the "winter fattening strategy". The constant morning mass model is characterized by seasonally constant mass recorded during the early morning, but a significant increase in evening body mass in winter compared to summer. The winter fattening model is characterized by both increased morning and evening body mass in winter-acclimatized birds relative to summer-acclimatized birds. Both seasonality of daily mass amplitude and daily minimum mass must be measured to separate between the two models (Lehikoinen 1987).

Body mass and fat data for birds in the family Paridae are equivocal. In addition to being tree-foraging species, many parids also cache food throughout the fall and winter (Bent 1946, Haftorn 1956) which might reduce the need for increased morning body fat in these birds. Body mass of five species of European parids followed the winter fattening strategy (Haftorn 1989) whereas Black-capped Chickadees (*Poecile atricapillus*) from New York, South Dakota, and New Jersey appear to have constant morning body mass with daily increases in body mass that do not vary seasonally (Chaplin 1974, Cooper and Swanson 1994, Graedel and Loveland 1995). They do not appear to follow the constant morning mass model since their average body mass in winter is not higher than in summer. Morning body mass and lipids do not vary seasonally in Mountain Chickadees (*Poecile gambeli*) or Juniper Titmice (*Baeolophus ridgwayi*), but diurnal changes in mass and lipids were not measured by Cooper (2002). Chaplin (1974) recorded both morning and evening body mass and lipid mass for Black-capped Chickadees during fall, winter, and spring. Body mass increased throughout the day, but seasonal differences in morning or evening body mass were not evident. Lipid mass also increased throughout the day and was significantly higher in evening in winter compared to fall or spring. North American parids do not appear to undergo true winter fattening and it is also unclear if they fit the constant morning mass model or use some other strategy regarding regulation of body mass.

My objectives were to measure seasonal and diurnal patterns of body mass and visible fat stores in Mountain Chickadees and Juniper Titmice to examine if they undergo winter fattening. These two species are small, largely non-migratory parids that occupy regions of western North America. They have behavioral adaptations, including food caching and cavity roosting (Bent 1946), and use regulated bouts of nocturnal hypothermia (Cooper and Gessaman 2005), which reduce costs associated with temperate overwintering. Since behavioral adaptations and nocturnal hypothermia reduce energetic costs, and because chickadees and titmice are tree-foraging birds, they may not have marked seasonal winter fattening.

METHODS

I captured Mountain Chickadees and Juniper Titmice in mist nets in Box Elder and Cache counties, Utah in summer and winter from 1995 to 1997. I used birds captured within 1 hr of sunrise in the present study. Timing of sunrise was obtained from U.S. Naval Observatory data. I measured body mass upon capture to the nearest 0.1 g with a portable electronic balance (Ohaus CT-1200), along with visible fat scores in abdominal and furcular regions using a scale of 0–5 (Helms and Drury 1960). I followed the recommendations of Rogers (1991) to reduce sources of error associated with scoring visible fat. Birds were transported following capture to the laboratory where they were housed individually in 30 × 25 × 30 cm cages inside a 3 × 3 × 2.5 m temperature-controlled environmental chamber. The chamber temperature and photoperiod followed a cycle that approximated the season and study site at which the birds had been captured. Birds were provided free access to water, grit, and food (*Tenebrio* larvae and black-oil sunflower seeds). Body mass and visible fat scores were obtained for all individuals within 15 min of sunset and again the morning after capture (within 15 min of sunrise). Thus, body masses and visible fat scores were recorded at three separate times during the day; at capture, sunset or evening, and the following or second morning. Birds measured from 15 July to 30 August were designated "summer birds" and those measured from 20

TABLE 1. Seasonal values (mean ± SD) of body mass and visible fat scores for Mountain Chickadees and Juniper Titmice. Sample sizes are in parentheses.

	Mountain Chickadee		Juniper Titmouse	
Measurement	Summer	Winter	Summer	Winter
Body mass (g)				
At capture	10.9 ± 0.5 (13)	11.0 ± 0.8 (19)	17.0 ± 1.2 (16)	16.4 ± 0.8 (10)
Evening	11.7 ± 0.5 (13)	12.0 ± 1.0 (19)	18.3 ± 1.2 (16)	17.4 ± 1.0 (10)
2nd morning	10.8 ± 0.5 (13)	11.0 ± 0.9 (19)	17.2 ± 1.3 (16)	16.1 ± 1.0 (10)[a]
Visible fat score				
Furcular				
At capture	0.46 ± 0.52 (13)	0.74 ± 0.81 (19)	0.25 ± 0.45 (16)	0.20 ± 0.42 (10)
Evening	1.85 ± 0.69 (13)	2.53 ± 1.07 (19)[a]	1.38 ± 0.50 (16)	1.50 ± 0.71 (10)
2nd morning	0.62 ± 0.51 (13)	1.11 ± 0.87 (19)	0.63 ± 0.50 (16)	0.20 ± 0.42 (10)
Abdominal				
At capture	0.38 ± 0.51 (13)	0.37 ± 0.50 (19)	0.06 ± 0.25 (16)	0.10 ± 0.32 (10)
Evening	1.23 ± 0.44 (13)	1.89 ± 0.81 (19)[a]	1.25 ± 0.45 (16)	1.50 ± 0.71 (10)
2nd morning	0.08 ± 0.28 (13)	0.37 ± 0.60 (19)	0.25 ± 0.45 (16)	0.20 ± 0.42 (10)

[a] Significant difference in seasonal intraspecific comparisons ($P < 0.05$).

November to 20 February were designated "winter birds."

All data are presented as means ± SD. Seasonal means of body mass and visible fat scores were compared by two-way ANOVA using season and time of day as independent variables. Student's *t*-tests were used for pairwise comparisons if significant seasonal effects were detected. Repeated-measures ANOVA was used to test for time of day effects as body mass and visible fat scores were recorded at three times during the day for each individual. Bonferroni's test was used to identify where differences occurred where a significant time of day effect was noted. Sequential Bonferroni alpha values were calculated according to the number of variables to establish statistical significance for the entire analysis (Rice 1989). Statistical significance was accepted at $P < 0.05$. All statistics were computed with SPSS 13.0 (SPSS Institute 2004).

RESULTS

There were no seasonal differences ($F_{1,90} = 1.77$, $P = 0.19$) (Table 1) in body mass data of chickadees but there were diurnal differences ($F_{2,90} = 15.41$, $P < 0.001$). Analysis of body mass data for titmice revealed seasonal ($F_{1,72} = 10.02$, $P < 0.01$) and diurnal differences ($F_{2,72} = 8.90$, $P < 0.001$). Visible fat scores in chickadees varied by season (abdominal fat: $F_{1,90} = 6.95$, $P = 0.01$; furcular fat: $F_{1,90} = 8.31$, $P = 0.01$) and time of day (abdominal fat: $F_{2,90} = 50.41$, $P < 0.001$; furcular fat: $F_{2,90} = 34.57$, $P < 0.001$). Visible fat scores varied only with time of day in titmice (abdominal fat: $F_{2,72} =$

TABLE 2. Repeated measures analysis of variance for time of day effects on body mass and visible fat scores for seasonally acclimatized Mountain Chickadees and Juniper Titmice.

				Visible fat scores			
	Body mass			Furcular		Abdominal	
Season	df	*F*	*P*	*F*	*P*	*F*	*P*
Summer							
Chickadees	2, 24	89.45	<0.001	48.67	<0.001	27.49	<0.001
Titmice	2, 30	108.76	<0.001	32.59	<0.001	66.13	<0.001
Winter							
Chickadees	2, 36	149.50	<0.001	100.61	<0.001	81.83	<0.001
Titmice	2, 18	79.48	<0.001	49.06	<0.001	28.89	<0.001

63.94, $P < 0.001$; furcular fat $F_{2,72} = 41.48$, $P < 0.001$). Body mass in titmice was lower ($t_{24} = -2.20$, $P = 0.038$) on the second morning in winter compared to summer. Body mass did not vary for titmice at capture ($t_{24} = -1.42$, $P = 0.17$) or during the evening ($t_{24} = -1.83$, $P = 0.080$) (Table 1). Visible fat scores were higher in the evening for winter chickadees compared to summer (abdominal: $t_{30} = -2.69$, $P = 0.012$; furcular: $t_{30} = -2.182$, $P = 0.037$). Visible fat scores did not vary in chickadees at capture ($t_{30} = -1.08$, $P = 0.29$) or recorded on the second morning ($t_{30} = -1.81$, $P = 0.080$) (Table 1).

Body mass and visible fat scores varied significantly due to time of day in chickadees and titmice in summer and winter (Table 2). Body mass expressed as percent mass increase from morning to evening was 7.3% for summer chickadees, 7.6% for summer titmice, 9.1% for winter chickadees, and 6.1% for winter titmice. Evening body mass was higher than mass at capture (Bonferroni, $P < 0.001$) and the second morning (Bonferroni, $P < 0.001$) for summer and winter chickadees. Body mass at capture did not vary significantly compared to the second morning body mass in summer or winter chickadees. Evening body mass for titmice was higher than mass at capture (Bonferroni, $P < 0.001$) and the second morning (Bonferroni, $P < 0.001$) in both summer and winter. Body mass at capture did not vary significantly compared to the second morning body mass in summer or winter titmice. Winter chickadees and titmice, relative to their summer counterparts, had significantly higher evening abdominal and furcular fat scores than fat scores at capture (Bonferroni, $P < 0.001$) and from the second morning (Bonferroni, $P < 0.001$). Fat scores at capture did not vary compared to the second morning in summer or winter for either chickadees or titmice.

DISCUSSION

Mountain Chickadees and Juniper Titmice do not appear to follow the constant morning mass or winter fattening models of Lehikoinen (1987). Mean body mass at capture and in the evening did not vary seasonally in either chickadees or titmice. In addition, mean body mass for titmice was significantly lower on the second morning in winter compared to summer. This decreased second morning body mass of winter-acclimatized titmice may be due to increased length of overnight fasting compared to summer. It may also be due to reduced eating by captive titmice in winter relative to summer. If this occurred, the evening body mass of winter titmice may have been underestimated. However, this does not affect the initial capture mass which did not show any seasonal variation. The body mass at capture data agree with that from other studies of North American parids (Chaplin 1974, Cooper and Swanson 1994, Graedel and Loveland 1995, Cooper 2002). Daily mass gains ranged from 6.1 to 9.1% in Mountain Chickadees and Juniper Titmice. These increases in evening body mass agree closely with data from Black-capped Chickadees (Chaplin 1974) and for several species of European parids (Haftorn 1992). Diurnal variation in body mass and visible fat scores was clearly evident in both chickadees and titmice. Visible fat stores for winter-acclimatized chickadees were significantly higher in evening compared to summer despite not having a significant increase in maximum evening mass. Higher evening fat without differences in body mass for winter birds has also been reported in Black-capped Chickadees (Chaplin 1974). Thus, increased amounts of fat may not be detected by measuring mass of birds. This has also been observed for Golden-crowned Kinglets (*Regulus satrapa*) (Blem and Pagels 1984).

Body mass at capture data from the present study conflicts with data from five European species of parids measured in Norway, which appear to follow a winter fattening strategy (Haftorn 1989). One possible difference is that Haftorn (1989) recorded body mass of individuals that landed on an electronic balance that served as a feeder. Birds in my study were held in captivity in individual cages which may have impacted their normal feeding behavior. However, Black-capped Chickadees recorded in the same manner as European parids also failed to show winter fattening (Graedel and Loveland 1995).

What other factors differ between North American and European parids that may explain the apparent differences in body mass strategies? Increased morning body mass and corresponding fat reserves benefit winter birds by providing more energy reserves that can be used when foraging is not possible. However, a generally assumed cost of elevated body mass and fat is an increased risk of predation (Lima 1986, Witter and Cuthill 1993, Lilliendahl et al. 1996). In Greenfinches (*Carduelis chloris*) from Sweden, the daily gain in body mass was lower for birds exposed to a stuffed flying hawk three times per day compared to no exposure to the perceived predator (Lilliendahl 2000). Thus, predation risks may vary by location in parids, which could change the daily mass strategy used by these birds. Another factor that may affect results of the North American studies compared to those of Haftorn (1989, 1992) is latitude. European parids that have been measured were in Norway at much higher latitudes than any North American parids. Thus, European parids that have been measured may have been exposed to harsher winter climates than their North American counterparts. However, chickadees and titmice used in my study were from altitudes of 1,700–2,300 m and were exposed to low ambient temperatures (Cooper 2002).

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The Wilson Journal of Ornithology 119(4):725–729, 2007

Effects of the First Southern Atlantic Hurricane on Atlantic Petrels (*Pterodroma incerta*)

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ABSTRACT.—We report a massive inland displacement of petrels, particularly female Atlantic Petrels (*Pterodroma incerta*) in southern Brazil, after Hurricane Catarina, the first ever reported hurricane in the South Atlantic Ocean. At least 354 petrels were affected and were found in 26 different locations, up to 420 km from the coast and 1,100 m above sea level. Birds were in heavy molt and near starvation, which probably contributed to their displacement and mortality. *Received 2 October 2006. Accepted 4 March 2007.*

The Atlantic Petrel (*Pterodroma incerta*) is a medium-sized gadfly petrel endemic to Gough and Tristan da Cunha islands (Brooke 2004); it has vulnerable global status (Birdlife International 2004) and is one of the least known seabirds (Cuthbert 2004). The global population is ~1.8 million pairs and declining because of low breeding success (20%) due to predation by introduced house mice (*Mus musculus*) on Gough Island (Cuthbert 2004, Cuthbert and Hilton 2004). It is also predated by Southern Skuas (*Stercorarius antarcticus*) on Gough Island and by rats (*Rattus* spp.) on Tristan da Cunha Island (Birdlife International 2004). The pelagic distribution is largely confined to the South Atlantic Ocean with a few records in the Indian Ocean (Enticott 1991, Brooke 2004). Distribution records range from 01° 31′ S, 38° 46′ W off Brazil (Bourne and Curtis 1985) to 65° 12′ S, 41° 05′ W in the Weddell Sea (Orgeira 2001) with most between 20 and 50° S (Enticott 1991). The species is most abundant close to the Subtropical Convergence Zone (Rumboll and Jehl 1977, Veit 1995).

Hurricanes, also called cyclonic storms, typhoons, or cyclones can have severe impacts on populations of vertebrates and invertebrates reducing abundance or extinguishing small populations, as well as extirpating them in more exposed areas (Spiller et al. 1998). Effects on terrestrial birds could be direct, such as death when exposed to strong winds and rain, and displacement to offshore waters or indirect, by increasing predation rates, destruction of nesting and roosting areas, and reduction of food resources (Wauer and Wunderle 1992, Wiley and Wunderle 1993, Collazo et al. 2003, White et al. 2005). The main effects of hurricanes on seabirds are loss of eggs, and mortality of chicks and adults with reduction of breeding success of terns (*Sterna* spp.) and noddies (*Anous* spp.) (White et al. 1976, Langham 1984), direct mortality of adults caused by strong winds (Cely 1991) or petrels and shearwaters displaced inland, particularly in North America (Murphy 1936, Heintzelman 1961, Wiley and Wunderle 1993). Birds found inland are apparently entrapped in the eye of hurricanes and are held away from the periphery of gales (Murphy 1936).

We describe the inland displacement of seabirds after Hurricane Catarina, which hit southern Brazil in March 2004 and provide data on biometry, molt, and body condition of affected Atlantic Petrels. Hurricane Catarina was named after Santa Catarina State in southern Brazil (Fig. 1) and was the first ever reported hurricane in the South Atlantic Ocean (Pezza and Simmonds 2005). It began as an extra-tropical cyclone 800 km from the coast of Brazil (26° S) ~20 March 2004 with minimal pressure inside the eye of 974 hPa (hectoPascal) and a total diameter of 400 km (Pezza and Simmonds 2005). It reached the

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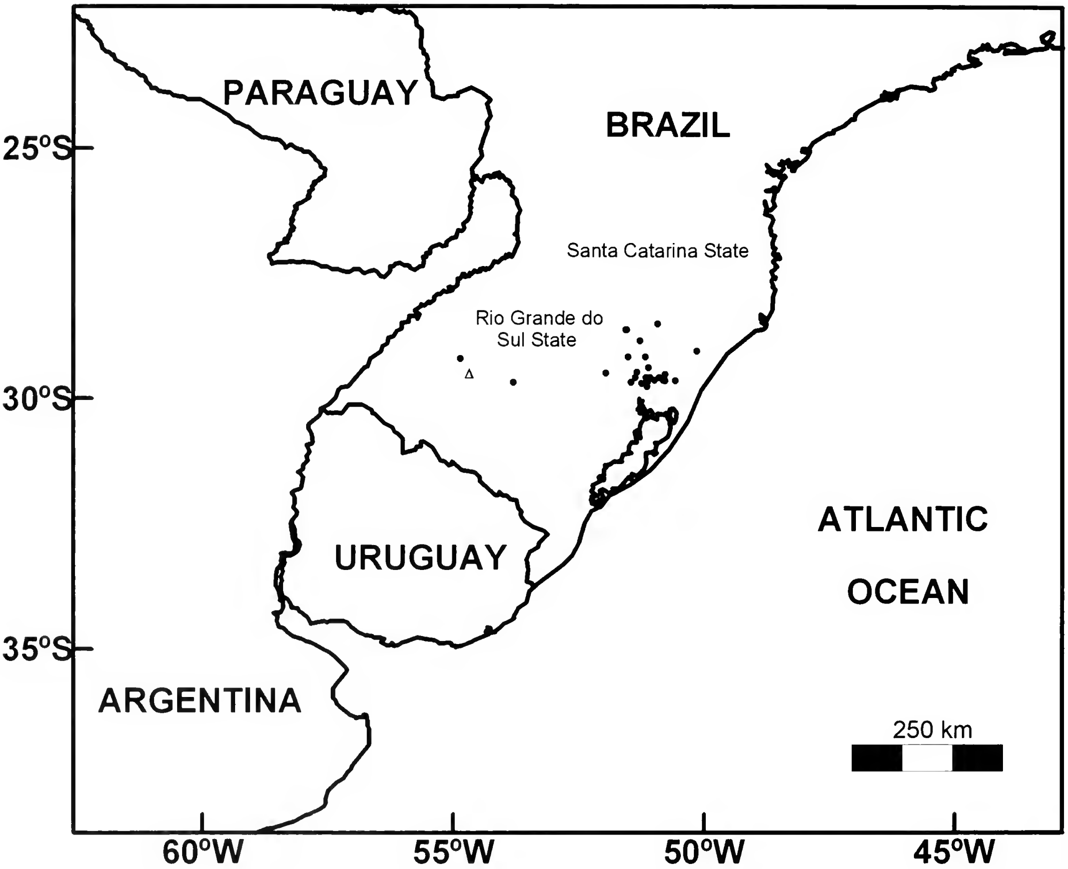

FIG. 1. Inland localities where Atlantic Petrels (dots) and Spectacled Petrel (triangle) were found in Rio Grande do Sul State, southern Brazil after Hurricane Catarina in March 2004.

coast of Rio Grande do Sul and Santa Catarina states on 28 March 2004 with winds from 119 to 153 km/hr and was classified as Category I according to the Saffir-Simpson scale (Pezza and Simmonds 2005). According to local newspapers, the winds destroyed 33,000 houses on the Brazilian coast and sank two fishing vessels in offshore waters.

METHODS

Data where birds were found were obtained by contacting rehabilitation centers. Standard measurements (Proctor and Lynch 1993) and molt status of 29 Atlantic Petrels were recorded, and body condition was assessed by necropsies. Measurements are provided as mean ± standard deviation, range, and sample size (*n*). Wing and tail measurements were not taken from birds molting the outer primaries or central tail feathers, respectively.

OBSERVATIONS

The Atlantic Petrel was the main species affected by Hurricane Catarina. One hundred and twenty-nine Atlantic Petrels and one Spectacled Petrel (*Procellaria conspicillata*) were found inland in Rio Grande do Sul State in an area ~300 km wide and up to 420 km from the coast. They were distributed from sea level to 1,100 m in 26 municipalities of Rio Grande do Sul State (Fig. 1). A flock of 50 Atlantic Petrels also was recovered in a freshwater reservoir used for hydroelectric power production, 190 km from the coast. In addition, another 225 petrels were reported inland in nearby Santa Catarina State, including Giant Petrels (*Macronectes* sp.) and Prions (*Pachyptila* sp.) for which specific identifications were not obtained. Birds from Rio Grande do Sul State were cared for at rehabilitation cen-

TABLE 1. Measurements (mm) and body mass (g) of Atlantic Petrels (*Pterodroma incerta*) displaced inland after Hurricane Catarina in southern Brazil in March 2004. Measurements of males (n = 6) and females (n = 23) were pooled.

	Mean ± SD	Range	n
Total length	416.6 ± 6.8	404–423	9
Wingspan	1,100 ± 20.3	1,080–1,130	5
Wing	323.1 ± 7.7	310–332	7
Tail	134 ± 11	122–154	11
Culmen length	38.1 ± 1.9	35.8–41.3	29
Tarsus length	45.4 ± 1.8	42.4–51.3	29
Body mass	344.6 ± 25.2	310–410	23

ters, but all Atlantic Petrels died within 2 weeks; only the Spectacled Petrel was released back to sea after 10 days. A minimum of 354 birds was recorded, but probably many more were displaced inland undetected.

Measurements of males and females were pooled (Table 1) because they overlap considerably (Cuthbert 2004). Necropsy of birds revealed the Atlantic Petrels were severely emaciated with mean body mass of 344.6 ± 25.2 g (Table 1) and no fat storage. No abnormality of internal organs was macroscopically detected and parasite infections were recorded in the digestive tract of only two birds from 23 examined.

The sex ratio was strongly biased to females (6 males, 23 females; $\chi^2_{\text{Yates}} = 8.83$, $P = 0.003$, df = 1). Females had enlarged ovaries (1–2 mm in length) and 28 of 29 birds were in heavy molt. Twenty-three of 29 birds were molting P9 and/or P10, 26 were molting rectrices (1 to 6 pairs molting simultaneously), and 28 birds (96.6%) had contour body molt. Birds were molting a larger number of rectrix feathers than primary feathers and the pattern of primary molt was more symmetrical than tail molt.

DISCUSSION

To our knowledge, this is the largest number of pelagic seabirds killed by a hurricane, comparable only to the death of 200–400 Brown Pelicans (*Pelecanus occidentalis*) following Hurricane Hugo in 1989 (Cely 1991). This event is not rare in the North Atlantic Ocean where both hurricanes and seabirds in inland areas are more common. Some examples are a Black-capped Petrel (*Pterodroma hasitata*) captured alive in August 1893 in Virginia, USA 2 days after a cyclone. It was found in a fish pond 320 km from the coast and 700 m above sea level, in final molt stage and starving (Smyth 1893). Murphy (1936) described records of Trindade Petrel (*P. arminjoniana*) displaced to Ottawa, Ontario and Ithaca, New York. Heintzelman (1961) recorded a Kermadec Petrel (*P. neglecta*) at Hawk Mountain Lookout, Pennsylvania, USA after Hurricane Gracie in October 1959. In addition, at least three emaciated Atlantic Petrels were collected from a hydroelectric power dam in the eastern Brazilian Amazonia in September 1984 (03° 50′ S, 49° 45′ W), 400 km from the nearest open sea and over 2,000 km from their normal area of occurrence in the western Atlantic Ocean (Teixeira et al. 1986). Overall, *Pterodroma* petrels appear to be more prone to be affected by hurricanes in comparison with other pelagic seabirds.

Measurements were in the range of 54 birds for which data were available from Gough Island (Swales 1965) with the exception of the tarsus, which was consistently longer than for birds from Gough Island (39.1 ± 1.6, 35–43 mm). However, tarsus length in Brazil agrees with 13 males and females measured by Murphy and Pennoyer (1952), which were in the range of 42.1–45 mm. All measurements were in the range for breeding birds provided by Cuthbert (2004). Differences in tarsus length provided by Swales (1965) in comparison with those reported by Murphy and Pennoyer (1952), Cuthbert (2004), and the present study were probably due to different measurement methods.

The mean body mass of birds affected by Hurricane Catarina of 344.6 g (310–410 g) was well below the 522.0 g (440–595 g) reported by Swales (1965) and the 544.4 g (420–720 g) reported by Cuthbert (2004) for birds on Gough Island. Thus, the birds appear to have been starving and could have been suffering from effects of the hurricane for several days. Atlantic Petrels feed largely on squid (87% by mass) (Klages and Cooper 1997) and those examined had obviously not been feeding for several days when inland.

The larger number of females in the sample could be due to differences in at-sea distribution or differences in body condition making females more vulnerable to the storm. The

Atlantic Petrel is a winter breeding species arriving in colonies in late March and departing after 3–4 weeks for a pre-laying exodus of ~50 days (Cuthbert 2004). Most of the Atlantic Petrels were in heavy molt and petrels in general do not molt during their first year. This information, along with the enlarged size of gonads reported here, suggests that petrels found inland in Brazil were ready to return to colonies when they were entrapped by the hurricane. Early accounts of Tristan da Cunha islanders of birds arriving in colonies still molting (Elliot 1957) agree with our data and suggest that molt is completed during the exodus period and before egg laying, which occurs from 15 June to 21 July (Cuthbert 2004).

Patterns of primary molt were more symmetrical than tail molt, consistent with their vital importance for flight in comparison with tail feathers. Langston and Rohwer (1996) suggested that worn feathers or heavy molt could be dangerous, particularly during storms, and Kinsky (1968) suggested that a stranding of 40 Shy Albatrosses (*Thalassarche cauta*) in 1947 was due to heavy molt. Primary molt in petrels is commonly descendant (Marchant and Higgins 1990) and rectrix molt starts after primary molt (Ginn and Melville 1983). Atlantic Petrels displaced by Hurricane Catarina were in late molt stage, which probably was important in depletion of fat reserves and starvation.

Effects of hurricanes on seabird populations are poorly understood, but could be potentially severe when affecting large numbers of endangered species. Hurricanes in the South Atlantic Ocean are postulated to increase in frequency with global warming (Pezza and Simmonds 2005) with potential detrimental effects on endangered species.

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Observations of the Military Macaw (*Ara militaris*) in Northern Oaxaca, México

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ABSTRACT.—We report observations of a population of Military Macaws (*Ara militaris*) within the Tehuacán-Cuicatlán Biosphere Reserve in northern Oaxaca, Mexico during 2002–2004. Macaws used a series of barrancas for roosting and nesting, and foraged widely in surrounding areas. Most of the population of ~100 individuals could be counted flying to or from the major roosting areas of El Sabino Canyon and Barranca de Las Guacamayas. Reproduction appeared to be restricted to vertical cliffs of El Sabino Canyon. Most movements were associated with seasonal foraging and depended upon availability of fruits. *Received 26 August 2006. Accepted 15 March 2007.*

The Military Macaw (*Ara militaris*) occurs in México, Colombia, Venezuela, Perú, Ecuador, Bolivia, and Argentina (Forshaw 1983, Juniper and Parr 1998), and may have once existed in Guatemala. Isolated populations in México have been reported on the Pacific slope from southeastern Sonora and southwestern Chihuahua to Oaxaca and Chiapas, on the Gulf coast in Tamaulipas, and in central Mexico in San Luis Potosí, Estado de México, Querétaro, and Michoacán (Howell and Webb 1995, Iñigo-Elías 2000). Records in Oaxaca are scarce and up to 40 years old, although Binford (1989) reported the species as a rare resident. Recently, *A. militaris* has been found in two zones of the Tehuacán-Cuicatlán Biosphere Reserve; the canyons of the Sabino and Seco rivers within the jurisdiction of the Santa María Tecomavaca and Santa María Ixcatlán communities, respectively, in northern Oaxaca (Salazar 2001). We studied the species in the Biosphere Reserve from 2002 to 2005 to examine feeding and nesting areas, and seasonal movements.

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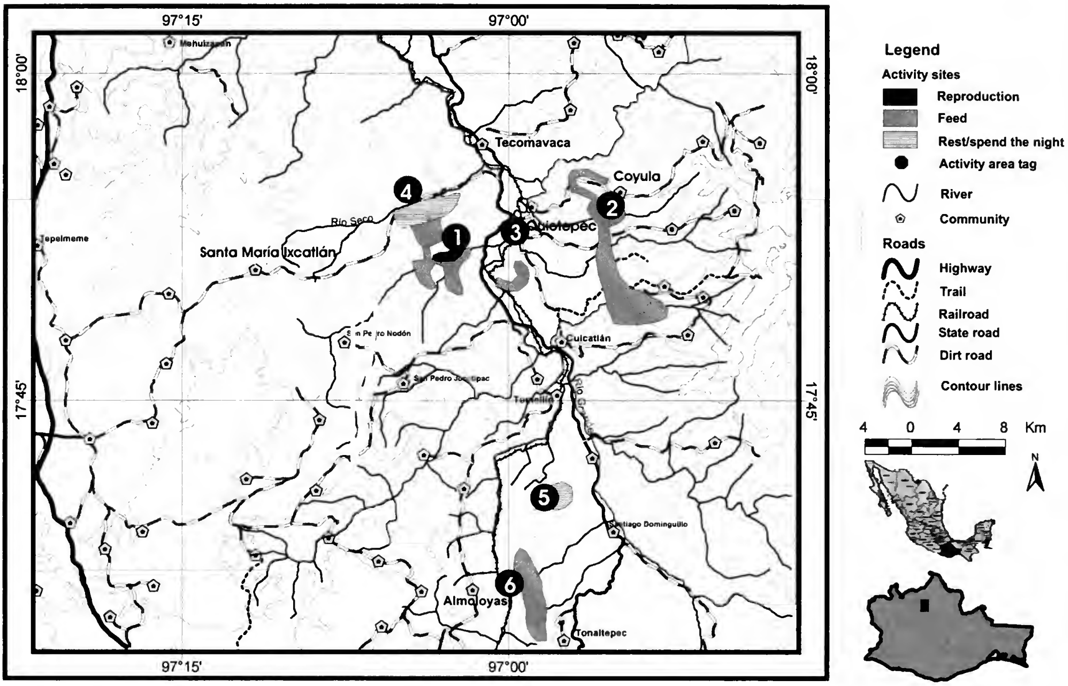

FIG. 1. Sites used by Military Macaws for roosting, reproduction, and foraging in the Tehuacán-Cuicatlán Biosphere Reserve in northern Oaxaca, México. (1) El Sabino Canyon, (2) Coyula, (3) Quiotepec, (4) Barranca de Los Compadres, (5) Barranca de Las Guacamayas, and (6) Almoloyas.

METHODS

The study area is within the Tehuacán–Cuicatlán Biosphere Reserve in northern Oaxaca, Mexico from 17° 30′ N to 18° 01′ N and 96° 50′ W to 97° 18′ W (Fig. 1). The topography of this area is complex, ranging from 520 to 2,850 m elevation. The area is part of the floristic provinces of the Tehuacán-Cuicatlán Valley (García and Torres 1999). We located areas used by macaws from ground surveys, and interviews with authorities and members of local communities. We conducted explorations and simultaneous observations at all sites between 2002 thorough 2004 to ensure that counts were from the same population, and to eliminate the possibility that more than one population was present. Each site was visited at least every third week for 2 days until all macaws had moved from the area. We chose an observation location with long distance visibility at each site to make population counts, and record daily movements between night roosting or nesting sites, and feeding sites.

OBSERVATIONS

Military Macaws primarily used the northern part of the study area from January until August for nesting and foraging. The most important sites used were El Sabino Canyon, Coyula, Quiotepec, and Barranca de Los Compadres. Macaws used the southern part of the study area from late September to December, primarily Barranca de Las Guacamayas for roosting at night and Almoloyas for foranging (Fig. 1). Macaws, like other psittacines, are gregarious, but movements between sites were not simultaneous. Instead, site use was low initially with only a few pairs observed, but within 2-3 months, the entire population could be counted (~100 individuals) at some sites.

El Sabino Canyon.—The Sabino River forms a deep canyon with walls 250 m high (17° 51′ 43.2″ N, 97° 02′ 37.5″ W) (Fig. 1). The predominant vegetation is tropical deciduous forest and xerophytic scrub (*tetecheras* and *cardoneras*). This is the only area where macaws have been observed to nest in the study area and was used mainly from January through September. The entire population uses this site for roosting at night from April into July and forages in adjacent areas from May through July. Nests occur in holes in the walls of the canyon, similar to those used by Maroon-fronted Parrots (*Rhynchopsitta terrisi*) (Macías 1998).

Coyula.—This is a small area leeward in the highest region of the Sierra de Juarez, south of the canyon of the Santo Domingo River, in an area that has continuously strong winds (17° 54′ 40.3″ N, 96° 56′ 11.5″ W) (Fig. 1). The vegetation in the area is a combination of tropical deciduous and humid oak (*Quercus* spp.) forest. These ecosystems differ in species composition from that commonly observed in the larger Oaxaca glen. The area is used by macaws from January through April for foraging during the morning and part of the afternoon. We have observed more than 50 individuals in this area, mostly during March and early April.

Quiotepec.—This area is near the dirt road connecting the towns of Quiotepec and Cuicatlán in proximity to the Grande River (17° 51′ 45.1″ N, 96° 59′ 13.9″ W) (Fig. 1). Habitats in this area are a mixture of riparian vegetation and lemon, mango, and anona plantations. It also contains tropical deciduous forest intermingled with xerophytic scrub from 50 to 100 m from the river. Columnar cacti such as *Myrtillocactus geometrizans*, *Pachycereus weberi*, and *Acacia cochliacantha* occur in the xerophytic scrub. This is a foraging area used during the day for some pairs from April through August. However, the entire population spends the night in El Sabino Canyon and forages in the surrounding areas. This is an intermediate area between Coyula and areas surrounding El Sabino Canyon.

Barranca de Los Compadres.—This area is on the old road to Santa María Ixcatlán (17° 54′ 9.1″ N, 97° 4′ 27″ W) (Fig. 1). It is characterized by vertical walls more than 100 m in height surrounded on the east by more or less flat surfaces and on the north by the Seco River. The predominant vegetation is tropical deciduous forest. This is a foraging and night roosting area used from July through October. Macaws primarily used two sites (Barranca de Las Guacamayas for night roosting and Almoloyas for foraging) south of the study area from late September to December.

Barranca de Las Guacamayas.—This area is a gorge with vertical walls of ~50 m southwest of the community of San José del Chilar (17° 40′ 44.6″ N, 96° 58′ 17.9″ W) (Fig. 1). The vegetation is mostly tropical deciduous forest. Macaws first arrive in this area in September and use it for night roosting until December. This area and El Sabino Canyon are the only sites where the entire population occurs together at a given time.

Almoloyas.—This area is in the southern part of Tomellin Canyon between the El Venado and Almoloyas railway stations (17° 38′ 15.7″ N, 96° 59′ 52.2″ W) (Fig. 1). The area contains tropical deciduous forest and xerophytic scrub, and is mostly natural as it is far from urban areas and roads. It has been identified as an isolated area with high endemism (Villaseñor et al. 1990, Dávila et al. 1995). It is used by the entire macaw population for foraging during those months when macaws roost in the Barranca de Las Guacamayas area.

DISCUSSION

The best and more consistent and robust counts of the population were in roosting sites because of the behavior of macaws in flying in morning to foraging sites and late in the afternoon to roosting sites. Thus, simultaneous observations can be used with confidence to identify the close relationship between areas used by macaws. There is no other known population of macaws to the north or south and there is no potential habitat to use to the west or east of the study area. We believe this population of *Ara militaris* is an isolated population.

The Military Macaw population in the areas surveyed is ~100 individuals. Macaws used feeding areas sequentially from the farthermost area east to that closest to El Sabino Canyon during the reproductive season in the first half of the year until they began to abandon the canyon from July to September. At this time, approximately half of the population spends the night in the Barranca de Los Compadres.

The first of the seasonal movements occurs at the end of the nesting season during August through October when the population leaves El Sabino Canyon and the Barranca de Los Compadres, and disperses over the region before joining in the Barranca de Las Guacamayas, south of the study area. The reverse movement occurs from January to April when the population joins in El Sabino Canyon.

The dominant vegetation in the area is deciduous forest and macaws may be found almost anywhere at any time of the year, but with obvious trends in use of some areas. The average maximum flight distance in a day is ~20 km allowing macaws easy access to a variety of resources and potential foods. We suspect that much of their flight activities provide information on the status of foods and it appears that macaws can readily take advantage of locally abundant food sources. However, they appear to be able to cope with irregularities in fruiting schedules of their major foods. Seasonal movements are the logical response to a diet based on fruit. The flexibility of movement patterns is also logical, given year to year fluctuations in plant productivity and the patchy distribution of important food plants throughout the range of macaws (Snyder et al. 1987). Seasonal movements are likely a response to breeding and availability of specific food resources similar to other psittacines (Symes and Perrin 2003).

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Juvenal Plumage in the Green-breasted Mountain-gem (*Lampornis sybillae*) with Observations on Timing of Breeding and Molt

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ABSTRACT.—We documented the juvenal plumage of the Green-breasted Mountain-gem (*Lampornis sybillae*) during mist-netting operations in the cloud forest at La Tigra National Park, Honduras from February to April 2006. A recently-fledged juvenile of this species was caught on 17 March and, contrary to previous suggestions, we found the throat and breast were mottled green. Ninety-eight immature mountain-gems intermediate between this juvenal plumage and that of adults were also caught during our study. Both males and females of the Green-breasted Mountain-gem apparently begin replacing juvenal throat feathers soon after fledging and prior to molting flight feathers. A high capture rate of young hummingbirds at the end of the dry season, including recent fledglings and individuals showing only traces of juvenal plumage, suggests a protracted breeding season that we estimate to last at least from November through March. We also caught adults in a variety of stages of flight-feather molt, perhaps part of a transition from breeding; molting in our population is estimated to span at least an 8-month period. *Received 25 October 2006. Accepted 19 January 2007.*

We conducted a preliminary survey of the avifauna of La Tigra National Park, Honduras in 2006 (Glowinski Matamoros 2006). No studies had been conducted in cloud forests of Honduras and little is known about avian species in this habitat, including hummingbirds. During mist-netting operations we identified juvenal plumage of the Green-breasted Mountain-gem (*Lampornis sybillae*) that differed from previous descriptions. Ridgway (1911) only described the adult plumage. Monroe (1968) questioned whether immature females have white throats while Howell and Webb (1995) report that immature males resemble the female "but throat whitish only faintly washed buff." Our observations did not match these descriptions and suggest they may be in error, perhaps from misidentification of museum specimens; alternatively, different subspecies could exist that are not currently identified.

The Green-breasted Mountain-gem is a fairly common resident of high elevation forests, especially cloud forest, and occupies both humid evergreen and pine-evergreen forest, and forest edge (Howell and Webb 1995). This species is largely restricted to Honduras and a small area of north-central Nicaragua, and is replaced by the closely related Green-throated Mountain-gem (*Lampornis viridipallens*) west of the Sula Valley (Monroe 1968). The status of these mountain-gems as two distinct species is based upon morphology and apparent differences in display patterns (Monroe 1963). Recent nuclear and mitochondrial DNA analysis failed to clarify the relationship (García-Moreno et al. 2006). Little is known about either species and the objective of this paper is to contribute to understanding the life history of tropical hummingbird species: we describe juvenal plumage in the Green-breasted Mountain-gem and present our observations on timing of breeding and molt.

METHODS

Mist-netting operations at La Tigra National Park, Honduras were conducted from 24 February to 19 April 2006 in primarily mid-successional cloud forest at an elevation of 1,700–1,800 m (14° 22′ N, 87° 08′ W). We caught birds toward the end of the dry season that typically lasts from December through April. Birds were not banded, but a small clipping of the outermost tail feather ensured that we were collecting data from different individuals. The unflattened wing chord was measured to the nearest half millimeter; the birds

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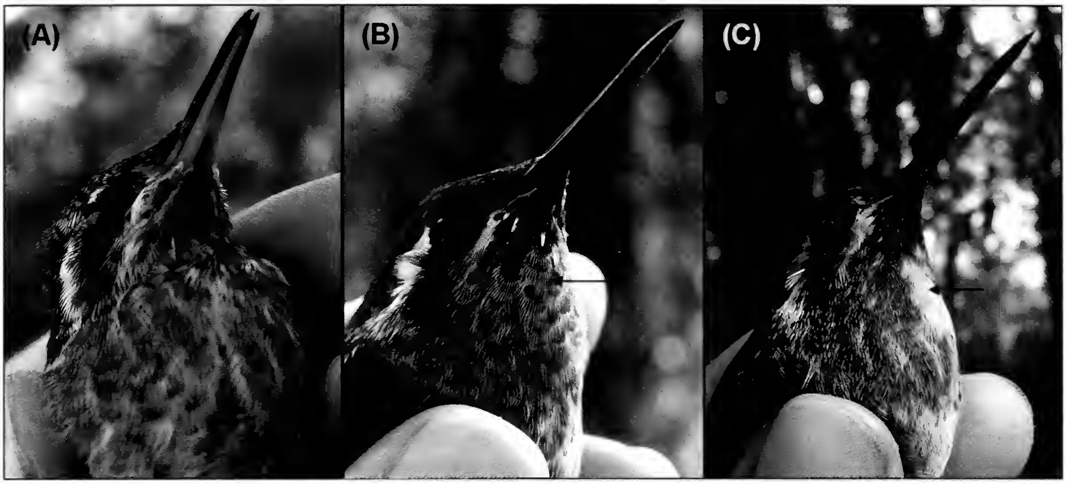

FIG. 1. Juvenile Green-breasted Mountain-gems captured in March 2006 at La Tigra National Park, Honduras. (A): a fledgling of unknown gender barely days out of the nest with the throat completely mottled green. (B): a young male has the start of iridescent green throat feathers. (C): a young female with a buffy patch on the throat. Photographs by Felicity L. Newell.

were then weighed with an electronic scale and checked for subcutaneous fat deposits. Flight feather molt was scored following Ginn and Melville (1983). We classified hummingbirds based on the extent of bill striations (Ortiz-Crespo 1972, Pyle 1997, Yanega et al. 1997). Breeding can occur year round in the tropics and it was not possible to ascertain the actual calendar year in which a bird was hatched, especially in February. We classified hummingbirds as immatures if distinct striations covered >50% of the bill. This would be equivalent to a bird in its first several months of life and prior to its first breeding season. We classified birds without obvious bill striations as adults. Birds captured were extensively documented with photographs.

OBSERVATIONS

We caught a fledgling Green-breasted Mountain-gem of unknown gender on 17 March 2006. Loud begging and an extensive yellow gape indicated this bird was recently out of the nest; all wing feathers (measured at 58.5 mm) and tail feathers were incompletely grown with the shaft still in sheath. The fledgling showed the white post-ocular stripe, green back, and dark inner rectrices with whitish outer rectrices distinctive of this species. The throat and breast were mottled green (Fig. 1A) similar to the green mottling on the sides and variably across the breast of adults. The bill was not fully grown in length and its underside was tinged dusky-pink near the base; adults have completely black bills.

Concurrently during mist-netting we caught 98 immatures (Fig. 1B, C) intermediate between the juvenal plumage described above and the adult plumage. Individuals ranged from juveniles with extensive green throat mottling and traces of pink under the bill to older birds with almost completely adult throat plumage and only a few retained juvenal feathers, typically just below the base of the bill. The mottling on juveniles appeared variable with almost solid dark green on some individuals. Young birds also had pale buffy to cinnamon edging on feathers of the crown and lower back. All immatures except the one fledgling showed distinct plumage dimorphism and gender could easily be identified based on incoming throat feathers alone, although there was also extensive sexual size dimorphism (Table 1). Both male and female Green-breasted Mountain-gems appear to begin acquiring adult throat plumage soon after fledging (a few young males had a more speckled but not full gorget). Rate of throat feather molt may vary as one male with an almost complete gorget still had pink under the bill but other males and females with mostly juvenal plumage had completely black

TABLE 1. Measurements of Green-breasted Mountain-gems captured at La Tigra National Park, Honduras, February–April 2006. Immatures had variable amounts of retained green mottling characteristic of juvenal plumage in this species. A few individuals (n = 15) had moderate fat deposits.

		Unflattened wing chord (mm)			Body mass (g)		
	n	Mean	SD	Range	Mean	SD	Range
Males							
Adults	51	67.1	1.5	64.5–69.5	6.0	0.4	5.3–7.3
Immatures	33	67.8	1.1	66.0–69.5	5.9	0.5	5.1–7.0
Females							
Adults	58	60.4	1.2	58.0–62.5	4.9	0.3	4.3–6.0
Immatures	65	60.9	0.9	59.5–62.5	4.7	0.4	3.9–5.7

bills. Some immature mountain-gems were also molting body feathers although none showed flight feather molt. Apparently both juvenal throat and body feathers in this species are replaced prior to flight feather molt; the extent and timing of this replacement remains unknown.

Indicative of active and/or recent breeding, half of the 207 Green-breasted Mountain-gems that we captured between 24 February and 19 April were immatures. We saw a similar trend for the other dominant species, the White-eared Hummingbird (*Hylocharis leucotis pygmaea*). A few immatures of other highland species included the Amethyst-throated Hummingbird (*Lampornis amethystinus*), Green Violet-ear (*Colibri thalassinus*), Magnificent Hummingbird (*Eugenes fulgens*), and Garnet-throated Hummingbird (*Lamprolaima rhami*). As well as immature hummingbirds, we also caught adults molting flight feathers, perhaps part of a post-breeding initiation of molt. During our mist-netting period, 29% (n = 109) of adult Green-breasted Mountain-gems were undergoing flight feather molt and individuals were captured with a range of molt scores (4–79). For other hummingbird species netted during this period, 49% of White-eared Hummingbirds (n = 100), 19% of Amethyst-throated Hummingbirds (n = 32), and 43% of Green Violet-ears (n = 14) were also undergoing flight feather molt.

DISCUSSION

The juvenal plumage that we observed in the Green-breasted Mountain-gem was consistent with the young of other hummingbird species in the genus *Lampornis*. Both the Blue-throated Hummingbird (*L. clemenciae*) and Amethyst-throated Hummingbird have a pinkish base to the lower mandible in juveniles. Based on the extent of bill striations, young of both of these species can also acquire nearly adult throat plumage (Pyle and Howell 2000; FLN, pers. obs.). Loose buffy edging on juvenal contour feathers is typical of immatures of many hummingbird species (Bent 1940, Williamson 2001). Our wing measurements consistently averaged ~2 mm larger than Ridgway (1911) reported from birds in Nicaragua. This could be due to measurement error, or geographic variation may exist within the species and northern individuals average slightly larger.

Breeding in tropical hummingbirds generally appears to be synchronized to local peaks in flower abundance either during the wet or dry season (Skutch 1950, Stiles 1980, Schondube et al. 2003). We confirmed breeding in March for the Green-breasted Mountain-gem with capture of a juvenile, and we estimated that some young fledged at least as early as December. This estimate is based upon several immatures captured in early April that still showed traces of juvenal plumage but which had lost most bill striations due to hardening and wear (Stiles and Wolfe 1974, Yanega et al. 1997). This suggests a protracted breeding season of 5 months or more in which females might attempt two broods.

The annual molt cycle in tropical hummingbirds may be complicated by regional variation and/or an extended breeding season (Wagner 1957). However, recent work suggests that in predictable seasonal environments such as cloud forests, adults should optimally molt following breeding (Barta et al. 2006). Our observations support post-breeding initiation of molt for adults at the end of the dry season. However, from a limited mist-netting period, it was not possible to ascertain that birds were not molting from August to November. We estimated the earliest molting Green-breasted Mountain-gems would have initiated molt around the beginning of December and the latest individuals completed molt by the end of July. Replacement of flight feathers in many hummingbird species typically takes 4 months or more (Williamson 1956, Stiles and Wolf 1974, Stiles 1980, Baltosser 1995). This would result in at least an 8-month period of molt within the population and is similar to the duration in several migrant species that depend on a seasonal environment (Williamson 1956, Baltosser 1995). Only in unpredictable environments have hummingbirds been found to molt year-round with timing following an individual 12-month schedule (Stiles and Wolf 1974).

The juvenal plumage of the Green-breasted Mountain-gem in our population was characterized by green mottling on the throat. Further work should examine whether the closely related parapatric Green-throated Mountain-gem may have similar juvenal plumage. More complete year-round study of the basic life history of this and other cloud forest species in Honduras and elsewhere is needed.

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Effect of Two Native Invasive Tree Species on Upland Pine Breeding Bird Communities in Georgia

Nathan Klaus[1,2] and Tim Keyes[1]

ABSTRACT.—Georgia land lottery maps from the 1820s reveal two tree species, water oak (*Quercus nigra*) and sweetgum (*Liquidambar styraciflua*), were formerly limited to major floodplains in the Piedmont and Coastal Plain. These species are now common in upland sites as a result of past land use and disruption of fire regimes. We investigated the effect this invasion had on breeding bird diversity in upland mixed pine (*Pinus* spp.) stands based on 90 point counts conducted in spring 2005. Half of these stands had no water oak or sweetgum (open stands) and half had a minimum of 25% of their basal area as water oak and/or sweetgum (invaded stands). Bird species richness and abundance were 42 and 41% lower, respectively, in invaded stands. Thirty-five bird species had more than 20 records and were tested for an association with invaded stands. No species were positively associated with invaded stands while 10 were negatively associated with invaded stands; these were mostly grassland pine savanna and shrubland bird species of high conservation value. Invasion of upland pine forest by these native tree species is similar to invasion by exotic species, and appears to disrupt ecosystem function causing declines in bird diversity. *Received 11 September 2006. Accepted 7 January 2007.*

Invasions by native species into novel habitats are often caused by human activity and have the potential for detrimental effects on local biodiversity similar to that from exotic invasive species (Myers 1985, Kupferberg 1996, McCay 2001). Examples are numerous and widespread (e.g., House Finch [*Carpodacus mexicanus*] eastward range expansion, bullfrog [*Rana catsbeiana*] range expansion and competitive exclusion of native frogs into the western United States, sand pine [*Pinus clausa*] invasion throughout the southeastern United States from forest industry plantings, and chickasaw plum [*Prunus angustifolia*] eastward introduction by Native Americans). Invasive exotic species are recognized as the second largest threat to biodiversity (Wilson 1992, Wilcove et al. 1998) following only habitat loss, yet effects of invasive native species remain largely unrecognized and unstudied.

Georgia land lottery maps from the early 1800s reveal a forest composition that is probably more similar, although possibly not identical, to prehistoric conditions and which is different from contemporary forests of the Piedmont and Coastal Plain (Nelson 1957). Changes in land use and fire regime following European immigration have caused many species to shift their distributions (Frost 1995, Cowell 1998, Lorimer 2001). One example is a substantial increase of water oak (*Quercus nigra*) and sweetgum (*Liquidambar styraciflua*) on upland sites. These species were absent from all but the floodplains of the largest rivers in the early 1800s. Land lottery maps indicate most Piedmont uplands were comprised of oaks, primarily post oak (*Quercus stellata*), and pine (*Pinus* spp.) while the coastal plain uplands were comprised of open stands of longleaf pine (*Pinus palustris*). Most of these forests were cleared in the late 1800s for agriculture. In the early 20th century, a period of farm abandonment began, which led to substantial re-growth of Georgia's forests (Brender 1974, Plummer 1975). The forest composition has changed, due to fire suppression, to a mixture of the original fire-dependent upland species of pine and oak, and fire-intolerant species including water oak and sweetgum (Cowell 1998). This forest type has been assumed to be a 'natural' upland forest type, although early researchers noted this change (e.g., Barrett 1943).

Unlike pines or upland oaks, leaves of water oak and sweetgum do not burn well and have the effect of suppressing fire. Both species are tardily deciduous and their leaves tend to lie flat, forming a cap on pine litter and other fuels that retain moisture, and act as a barrier to oxygen and heat. These species also have denser canopies, shading out the herba-

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ceous layer that is important for carrying fire. These characteristics have initiated a positive feedback cycle, whereby the presence of water oak and sweetgum further decreases fire frequency and intensity allowing these species to increase their dominance in upland ecosystems. We hypothesize that, by this mechanism, water oak and sweetgum have altered forest structure, species composition, fire regime, and wildlife habitat of upland ecosystems. We investigated the effect of upland invasion by water oak and sweetgum on the breeding bird communities of central Georgia in terms of bird species richness and abundance, and which species are positively and negatively related to the presence of water oak and sweetgum.

METHODS

Ninety sites were surveyed on four properties in the Piedmont (Oconee National Forest [33° 10′ N, 83° 48′ W], Brender Experimental Forest [33° 02′ N, 83° 43′ W], Rum Creek Wildlife Management Area [WMA] [33° 01′ N, 83° 47′ W], Sprewell Bluff Natural Area [32° 51′ N, 84° 28′ W]) and one in the Coastal Plain (three tracts of Mayhaw WMA [31° 10′ N, 84° 46′ W]). Sampling units were forest stands as designated by forest inventory data. The average stand size was 15 ha. All stands were former farm fields abandoned in the early 20th century that had naturally succeeded to loblolly pine (*P. taeda*) forest. Stands with at least 25% of their basal area in water oak or sweetgum (invaded stands) were paired with stands with an equal basal area of pine to the nearest 0.09 m^2/ha (10 ft^2/ac), and less than 5% of their basal area in water oak or sweetgum (open stands). Open and invaded stands were also paired by pine size category: dominant trees <25 cm diameter at breast height (DBH) or >25 cm DBH on average. All stands showed evidence of fire in the last 10 years, although fire frequency was variable and likely differed over the history of the stands.

Ninety 100-m, fixed-radius point counts (Hamel et al. 1996) were conducted (one/stand) between 15 May and 5 June 2005. Bird surveys were conducted for 10 min between sunrise and 1000 hrs. Bird survey stations between each stand were separated by at least 200 m, usually considerably more, and were at least 100 m from the stand edge when possible. Stands were considered independent of each other for purposes of this study.

Bird species richness (number of species detected/point) and abundance (number of individuals/point) were calculated by stand type. Analysis of variance (PROC MIXED, SAS 2003) was conducted on bird richness and abundance by stand type. Probability of detection by stand type was tested for all bird species with more than 20 detections between stand types. A measure of the relative bird conservation value of open and invaded stands was calculated by summing the Partners in Flight (PIF) combined breeding season

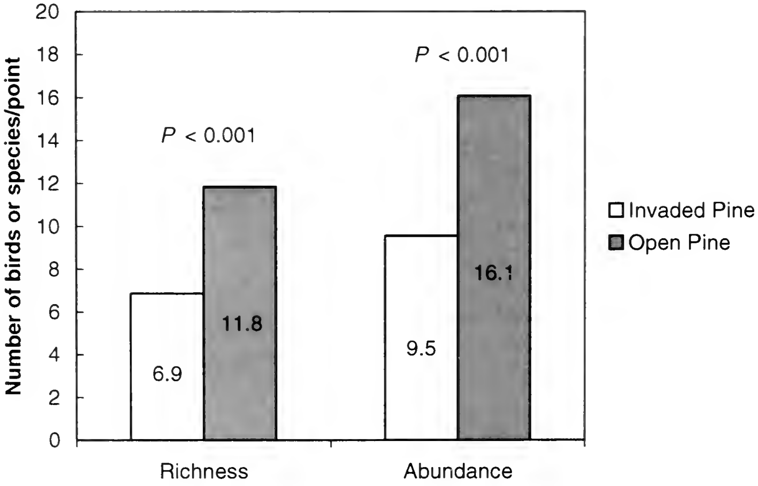

FIG. 1. Bird species richness and abundance in open and invaded Piedmont and Coastal Plain sites, Georgia.

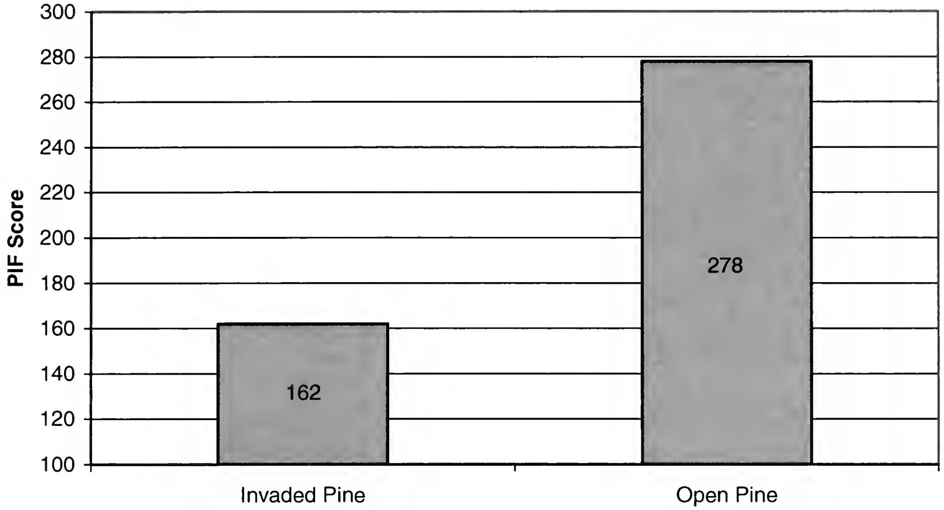

FIG. 2. Average summed Partners in Flight scores (bird conservation value) of invaded and open mixed pine stands in Piedmont and Coastal Plain sites, Georgia.

scores (Panjabi et al. 2005) of birds on each point and calculating the average of these scores by stand type.

RESULTS

We detected 954 individuals of 52 species across all points. Species richness averaged 11.8 species/point in open stands and 6.9 species/point in invaded stands (Fig. 1). Bird abundance was 16.1 individuals/point in open stands and 9.5 individuals/point in invaded stands. Richness and abundance were higher ($P < 0.001$) in open than invaded stands. Of 35 species that had more than 20 records, 10 were more common ($P < 0.05$) in open stands while no species were significantly more common in invaded stands (Table 1). Average conservation value was higher ($P < 0.001$) in open ($\bar{x} = 278$) than invaded stands ($\bar{x} = 162$) (Fig. 2). High conservation priority grassland and shrubland birds were negatively associated with presence of sweet gum and water oak.

DISCUSSION

Invasion of upland sites by water oak and sweetgum substantially lowered the number of bird species and individuals during the breeding season. Six of the top 10 species identified as high conservation priorities in Partners in Flight plans (Red-cockaded woodpecker [*Picoides borealis*], Bachman's sparrow [*Aimophila aestivalis*], Brown-headed Nuthatch [*Sitta pusilla*], Prairie Warbler [*Dendroica discolor*], Northern Bobwhite [*Colinus virginianus*], and Red-headed Woodpecker [*Melanerpes erythrocepahlus*]) declined or disappeared from upland pine stands when water oak and sweetgum comprised 25% or more of the canopy. Most species negatively associated with invaded sites were of two habitat guilds: grassland/pine savanna birds and shrubland birds. These groups have consistently shown the strongest population declines of all North American birds (Hunter et al. 2001).

The dense shade of water oaks and sweetgum reduced herbaceous and shrub cover, eliminating critical nesting and foraging habitat for many bird species. Invaded forests tended to have about half the plant species richness (invaded, $\bar{x} = 16$ species/m^2; open pine $\bar{x} = 26$ species/m^2; $P < 0.033$, $n = 6$) (L. Kruse, N. Klaus, and T. Keyes, unpubl. data), which may translate into reduced food resources for birds.

Most striking was that no bird species detected on our surveys was positively associated with invaded stands. This suggests that upland bird species have not specialized in upland pine stands dominated by water oak and sweetgum, and the invaded forest type may be an artifact of recent human land use. Reduction or elimination of sweetgum and water oak in upland mixed pine sites would improve habitat quality for declining grassland and shrubland birds, and may not negatively im-

TABLE 1. Species associations (+ or −, and *P* value from ANOVA) with invaded pine stands sorted by PIF breeding season score, Piedmont/Coastal Plain, Georgia.

Species	Scientific name	Invaded pine	Neutral	PIF score
Red-cockaded Woodpecker	*Picoides borealis*	(−) 0.089		23/20
Bachman's Sparrow	*Aimophila aestivalis*	(−) 0.003		21/18
Brown-headed Nuthatch	*Sitta pusilla*	(−) <0.001		20/18
Prairie Warbler	*Dendroica discolor*	(−) <0.001		18/18
Eastern Towhee	*Pipilo erythrophthalmus*		*	16/16
Northern Bobwhite	*Colinus virginianus*	(−) 0.117		16/16
Summer Tanager	*Piranga rubra*		*	16/15
Carolina Chickadee	*Poecile carolinensis*		*	16/15
Acadian Flycatcher	*Empidonax virescens*		*	15/15
Red-headed Woodpecker	*Melanerpes erythrocephalus*	(−) 0.030		15/13
Wood Thrush	*Hylocichla mustelina*		*	15/16
Yellow-billed Cuckoo	*Coccyzus americanus*		*	15/14
Yellow-throated Vireo	*Vireo flavifrons*		*	15/14
Pine Warbler	*Dendroica pinus*		*	14/14
White-eyed Vireo	*Vireo griseus*		*	14/11
Blue Jay	*Cyanocitta cristata*		*	14/13
Downy Woodpecker	*Picoides pubescens*		*	14/13
Indigo Bunting	*Passerina cyanea*	(−) 0.001		14/12
Pileated Woodpecker	*Dryocopus pileatus*		*	14/11
Carolina Wren	*Thryothorus ludovicianus*		*	13/13
Red-bellied Woodpecker	*Melanerpes carolinus*	(−) 0.003		13/12
Yellow-breasted Chat	*Icteria virens*	(−) 0.006		13/12
Common Yellowthroat	*Geothlypis trichas*		*	13/12
Tufted Titmouse	*Baeolophus bicolor*		*	13/12
Blue Grosbeak	*Passerina caerulea*	(−) 0.027		12/14
Great-crested Flycatcher	*Myiarchus crinitus*		*	12/10
Northern Cardinal	*Cardinalis cardinalis*		*	12/10
American Crow	*Corvus brachyrylncos*		*	11/12
Eastern Bluebird	*Sialia sialis*		*	11/11
Mourning Dove	*Zenaida macroura*		*	11/11
Red-eyed Vireo	*Vireo olivaceous*		*	11/10
Blue-gray Gnatcatcher	*Polioptila caerulea*		*	11/10
Chipping Sparrow	*Spizella passerina*		*	9/10
American Goldfinch	*Carduelis tristis*		*	8/10
Brown-headed Cowbird	*Molothrus ater*	(−) 0.010		8/10

* = No significant relationship to stand type.

pact any other breeding bird species during the breeding season. Other species of oaks, primarily post oak, southern red oak (*Quercus falcata*), and black oak (*Q. velutina*) were observed in both stand types but did not appear to have a negative impact on bird species' richness or abundance. These trees tolerate fire well, do not produce dense shade or reduce fire intensity, and are at least comparable in the quality of mast production to water oaks.

Water oak and sweetgum are native to the southeastern United States, Georgia, and even the particular watersheds in our study areas but are exotic in the upland pine ecosystem. Invasion of uplands by water oak and sweetgum follows a pattern similar to the spread of invasive exotic species; they create a positive feedback cycle whereby ecosystem function is altered which promotes their continued growth. This study demonstrates that in upland forests of central Georgia, invasion by native trees species into novel habitats is associated with a decline in bird species, particularly the most specialized species (e.g., grassland/shrubland birds). This results in a significant decrease in diversity from the former ecosystem.

Sweetgum and water oak are native to the southeastern United States but they are not native to all habitats. Management objectives for conservation lands should consider where dominance of these tree species is appropriate.

Conservation of the most vulnerable bird species may necessitate removal of these tree species from upland habitats.

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Turkey Vulture Nest Success in Abandoned Houses in Saskatchewan

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ABSTRACT.—Turkey Vultures (*Cathartes aura*) in southern and south-central Saskatchewan first nested in deserted houses in 1982. This new behavior across the Aspen Parkland and Boreal Transition ecoregions became more common in the mid-1990s as vultures increased and occupied new territory. We documented 126 nestings, which produced 185 young in 74 deserted buildings during 2003–2006. The mean number of young fledged per successful nest (1.7) was similar to that recorded in other parts of its range. *Received 25 April 2006. Accepted 11 March 2007.*

Turkey Vultures (*Cathartes aura*) began to nest in deserted buildings in the United States over a century ago, but use of this substrate increased slowly. As early as 1902 or 1903, one pair nested in a deserted pig-sty in western Pennsylvania (Jackson 1903). In 1927, a pair used the floor of an abandoned barn in South Carolina (Pickens 1927) and another used an abandoned granary in Ohio (Price 1928). The first nest in a building in Wisconsin was reported in 1977 with another eight known by 1991 (Mossman and Hartman 1992). The attic of an abandoned house in South Dakota was used in 1974 (Mossman 1991). Jackson (1983) reviewed 899 Turkey Vulture nest sites in North America through 1982 and reported a preference for "dark recesses"; however, only 22 of 838 (2.6%) nests were in deserted buildings, chiefly barns.

In Saskatchewan, all 13 published vulture nests through 1968 were in caves or on the ground. These, together with four pre-1900 records from major egg collections and 12 later (1968–1996) uses of natural substrates, are distributed across the settled portions of the province (Fig. 1), but are particularly related to major river valleys and mixed forest areas near lakes (Houston 1969, 2006). There were 23 known nestings in 15 caves and 17 one-time nests on the ground; one of the latter was in a large hollow log and the 10 most recent nestings, beginning in 1959, were in nearly impenetrable dense brush-piles.

The first reported instances of vulture nests in Saskatchewan in buildings were from attics of deserted farm houses in 1982 and 1983 (Beaulieu 1985, Wapple 1985, Houston 2006). Since 1995, Turkey Vultures have increased throughout Saskatchewan's Aspen Parkland and Boreal Transition ecoregions, coincident with this major change in nest substrate use. For example, in 2002, three pairs of Turkey Vultures nested in the Saskatoon area for the first time in recorded history (Houston et al. 2002), laying their eggs on the bare upstairs floor in deserted houses. Our objective in the present paper is to describe the use of deserted buildings by Turkey Vultures as nesting sites across southern Saskatchewan from 2003 to 2006.

METHODS

We located nesting vultures during 2003–2006 through landowners who responded to yearly newspaper articles in the *Western Producer* and three-times-a-year interviews with CSH on CBC radio across Saskatchewan. We investigated all nests reported but, to avoid any potential risk of desertion or of attracting common raccoons (*Procyon lotor*), we advised finders to stay away from nests until mid-July. We visited each nest once during the first 2 weeks of August to attach patagial tags (white letters on green Herculite; Houston and Terry 2003, Houston and Bloom 2005). Patagial tags were affixed to the wings of large but unfledged young, most of which were 50 or more days of age (Ritter 1983) with a wing chord of >390 mm. Landowners monitored some tagged young up to 6 weeks, until their departure.

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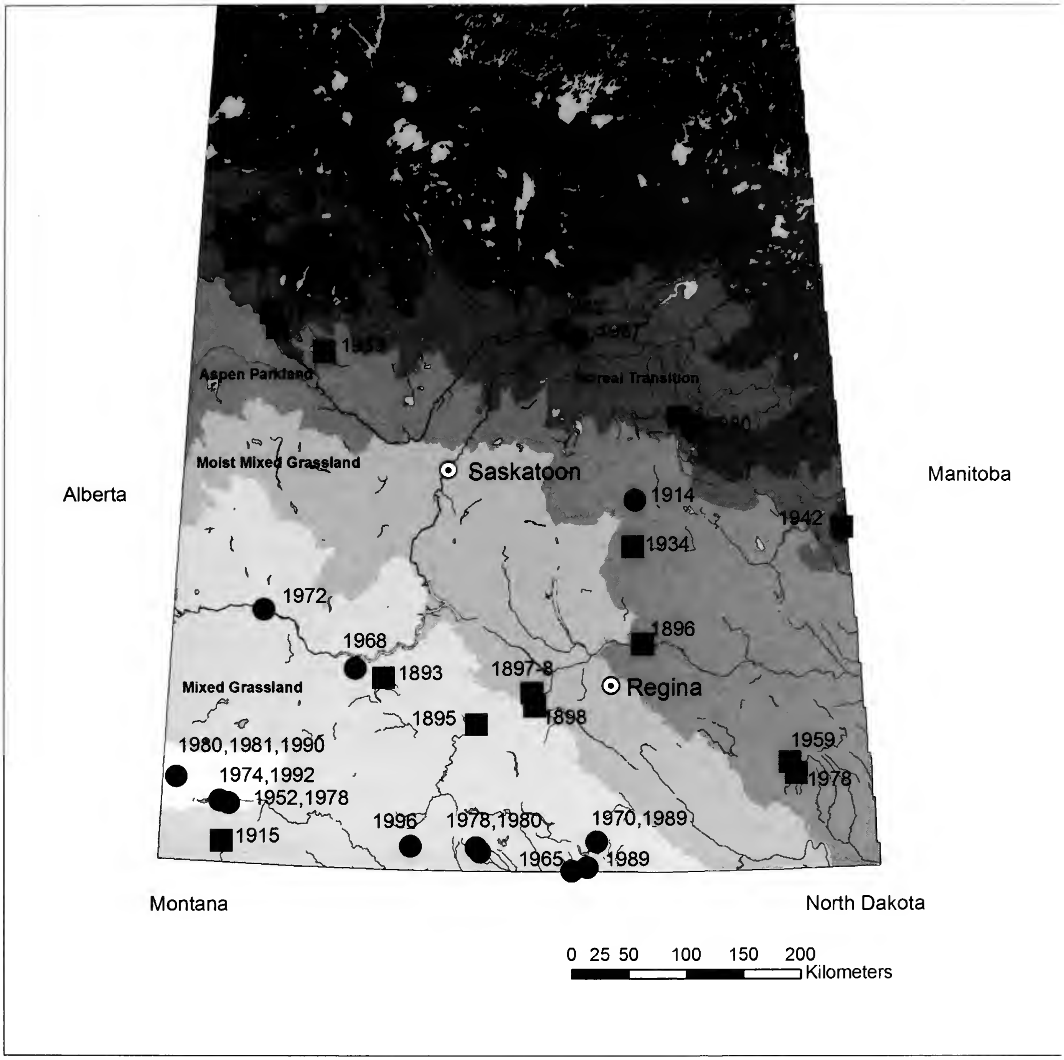

FIG. 1. Distribution of Turkey Vulture nests in natural sites (caves and brush-piles) in Saskatchewan, 1893–1996. Unshaded area in southwest represents Cypress Hills Upland Ecoregion. Circles indicate caves. Squares indicate ground nests.

RESULTS

We learned of 13 active nests in 2003 in vacant buildings. Vultures abandoned two of these nests: one in a barn in a deserted farmyard after a noisy, all-day family reunion and another where both young died because of the 3-day presence of a British documentary film crew. A single young in a small space below the flat roof of a full granary died of apparent dehydration during a hot spell. Seventeen young fledged from 10 buildings and host farmers reported that all vultures in nine nests fledged successfully. The outcome of the 10th nest was not known.

Twenty-two active nests were known in 2004. Half-grown young present in two nests on 15 July disappeared without a trace by 6 August, presumably from predation. Two other nests had only one and two unhatched eggs, respectively. Thirty-two young fledged from 18 vacant houses.

Thirty-eight active nests were located in 2005, including two just across the boundary in Manitoba and two on basement floors in

TABLE 1. Productivity of Turkey Vultures in southern Saskatchewan, 2003–2006.

Parameter	2003	2004	2005	2006	Totals
Minimum number eggs laid	20	39	55	97	211
Number unhatched eggs	0	3	3	5	11
Number eggs hatched	20	36	52	92	200
Number young dead in nest	3	4	4	4	15
Number young fledged	17	32	48	88	185
Nests with 1 young fledged	3	4	16	10	33
Nests with 2 young fledged	7	14	16	39	76
Number active nests	13	22	38	53	126
Number successful nests	10	18	32	49	109
Young fledged/active nest	1.3	1.5	1.3	1.7	1.5
Young fledged/successful nest	1.7	1.8	1.5	1.8	1.7
Number young fledged untagged	3	2	5	4	14

houses. Two nests contained only unhatched eggs, a single young died after falling 6 m through a hole in an attic floor, and three nests were presumed to have been depredated. Forty-eight young fledged from one barn and 31 vacant houses.

Fifty-three active nests, three of which were in barns, fledged 88 young in 2006. The six nest failures included two that may have been depredated; one nest with two unhatched eggs; two nests where the single young died, and another nest where two young died of suspected starvation but were too decomposed to necropsy.

During 2003–2006, 185 nestling Turkey Vultures fledged and the documented number of young fledged from deserted houses nearly doubled each year as a result of increased publicity (Table 1). The average number of nestlings fledged was 1.5/known active nest (n = 126 nests) and 1.7 young/successful nest (n = 109 nests). Seventy-six of 109 successful nests (70%) fledged two young and 33 (30%) fledged one young; 14 young vultures flew before they could be tagged. We noted 11 unhatched eggs, but do not know whether or not any nests failed during incubation. We assume mortality was minimal in the 1–2 weeks between tagging and first flight, as observers did not find tagged young dead in buildings. Apparent predation by raccoons was thought to be the cause of two nest failures in 2004 and three in 2005 (with circumstantial evidence, i.e., claw marks or scat at two nests). Our annual nest success of 77–90% does not account for nest failures that may have occurred before nests were found.

We photographed 61 occupied buildings, with 12 so overgrown by trees as to be invisible, 13 were enclosed on two or three sides, and 36 were readily visible in a relatively open landscape. We were unable to locate a single active vulture nest during 2003–2006 in substrates used in the past (caves and brush-piles); one pair was present along a 400-m long log-pile but the nest was not located.

DISCUSSION

Only one report from Saskatchewan suggests that vultures were common when bison (*Bison bison*) carcasses littered the western plains prior to about 1870 (Roe 1951:467–520). Walter Raine (1892:69) noted the species daily at Rush Lake in 1891. That year his Indian guide told him that Turkey Vultures had been "more numerous years ago, when he was a boy, and when the buffalo were plentiful on the prairie." A similar account in northeastern Montana by E. S. Cameron (1907:259), reported that vultures were "incredibly numerous" during the "prodigious slaughter of bison" as late as 1883 and 1887.

The expanded distribution of Turkey Vulture nest sites since 1982 (Figs. 1, 2) appears to represent a response to increasing availability of deserted houses. Apart from eight nests, most of our locations were not associated with river valleys, although water bodies are commonly present every 10 km throughout Aspen Parkland and Boreal Transition ecoregions.

Turkey Vultures also nest in buildings in adjacent provinces. However, in Manitoba,

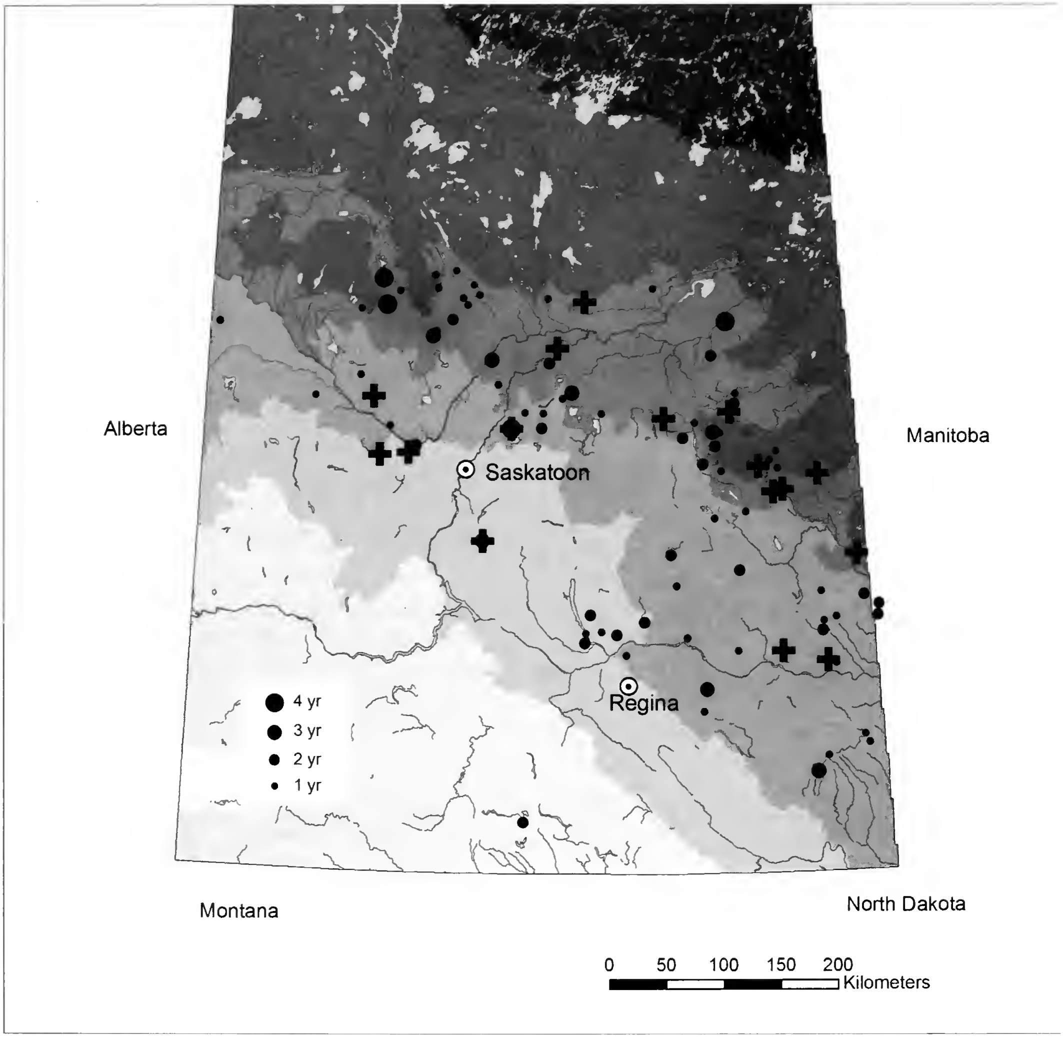

FIG. 2. Turkey Vulture use of deserted buildings in Saskatchewan, 1982–2006; + indicates use in 1982–2002. The largest dots (4) indicate buildings used in 4 successive years, 2003–2006. Dots of the next largest size (6) show buildings used in any 3 years. The second smallest dot (20) indicates buildings used in any 2 years while the smallest dot (44) indicates buildings used in 1 year.

birds remained concentrated along the Assiniboine River in the 1990s (Berezanski 1999), while in eastern Alberta all 14 buildings with nests were virtually hidden by aspen (*Populus tremuloides*) and other growth (Nelson et al. 2005). Saskatchewan has not experienced any appreciable northward range extension of nonbreeding birds (Smith 1996:96), as documented in British Columbia between 1890 and 2005 (Campbell et al. 2005).

Kirk and Mossman (1998:16) reported the "most important requirement of nest site [for Turkey Vultures] appears to be isolation from human disturbance." Deserted farm houses fit this definition as attics offer relatively secure nest sites. Many clearings around homesteads that are now deserted have been re-invaded by aspen, occasionally hiding the buildings. However, a semi-open area is usually immediately adjacent, which allows access by these large birds through an open window or a hole in the roof.

The yearly increase in the number of nests known to us is largely an artifact of publicity, which each year reaches new individuals. However, farmers, without exception, confirm that use of buildings as nest sites is a new phenomenon on their properties, observed for only 1–10 or rarely 12 years. These farmers report more and more vultures where none had been seen previously.

We did not study nest failures during incubation and cannot compare overall nest success with other studies. Our best measure of productivity, the number of young per successful nest (1.7), is similar to that in the Pennsylvania-Maryland area (1.7) and Wisconsin (1.8) (Kirk and Mossman 1998:19).

Nesting in buildings, deserted houses, and four uses of three barns, a new phenomenon dating from 1982, has allowed vultures to occupy territories in at least 100 Saskatchewan townships where natural substrates were rarely available. Concurrently, their numbers have increased, as evidenced by three observations. None was reported on Saskatchewan Breeding Bird Surveys (BBS) during 1968–1993, but six were observed on four BBS counts in 3 years, 1994–1997 and nine were observed on six counts in 4 years, 2002–2005 (A. R. Smith, pers. comm.). Five vultures were reported on the Saskatoon Annual Spring Bird Count in 2003, an all-time high. Phyllis Bordass (pers. comm.) reported 40 vultures soaring northeast over Fort Qu'Appelle during spring migration on 17 April 2006, apparently the largest migratory flock ever recorded in Saskatchewan.

The increasing number of deserted houses is the result of massive rural depopulation, which has increased the average Saskatchewan farm size from 149 ha in 1921 to 278 ha in 1961 and 520 ha in 2001. Saskatchewan's rural farm population decreased 15.2% in 5 years, from 145,560 in 1996 to 123,385 in 2001 (Statistics Canada 2006). Use of deserted buildings as nesting sites by Turkey Vultures has made these sites easy for us to access, and facilitated our studies of productivity and movements.

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Adult Yellow-crowned Night-herons Face in Opposite Directions at the Nest

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ABSTRACT.—Vigilance is especially important in colonial socially monogamous birds during the nesting season as nest materials, offspring, and mates are vulnerable to theft, depredation, and extra-pair copulations, respectively. We found that when both members of a mated pair of Yellow-crowned Night-herons (*Nyctanassa violacea*) were at the nest they faced in opposite directions in 73% of observations, which was significantly more often than would be expected by chance ($P < 0.0001$, $\chi^2_1 = 33.3$). This behavior may improve vigilance against intruders from all directions. When an extra-pair conspecific was present at the nest of a mated pair, members of the pair were significantly more likely to orient in the same direction towards the conspecific rather than face opposite directions. In 95% of all cases in which an extra-pair conspecific was present, at least one member of the mated pair faced it, indicating that extra-pair conspecifics are perceived as threats by nesting pairs. *Received 8 August 2006. Accepted 17 January 2007.*

Birds often benefit from colonial nesting. One of the most important advantages is shared threat surveillance in which predator detection by one member of the colony alerts other members of a potential threat (Lazarus 1979, Lima 1995, Roberts 1996). Another important benefit of living in a colony is predator dilution (Turner and Pitcher 1986, Inman and Krebs 1987). The overall level of predation may increase when bird density increases, but the probability that any particular individual will become prey decreases. These benefits can cause selection to favor colonial nesting.

Nesting in a colony also exposes birds to increased competition for limited resources. In many species, individuals expend both time and energy fighting over mates, territories, nesting materials, and food. These behaviors are exacerbated by the close proximity of other individuals in colonies (Caraco et al. 1980). Thus, natural selection on individuals may favor smaller or less dense colonies.

Most species in the family Ardeidae breed in dense colonies. However, Yellow-crowned Night-herons (*Nyctanassa violacea*) often nest individually or in dispersed colonies (Watts 1989). We have observed Yellow-crowned Night-herons breeding in small clusters of nests present at regular intervals throughout an area of about 3 ha. These dispersed colonies may be a result of opposing selection pressures, such as the risk of predation and cost of competition. It is likely both threat surveillance and predator dilution occur in dispersed colonies, but protection against predators of nestlings may be reduced with decreased colony size and density. Thus, one might expect natural selection to favor increased vigilance by mated pairs in dispersed colonies.

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We collected data on vigilance behavior in mated pairs of Yellow-crowned Night-herons during the breeding season. We addressed the following questions: (1) do members of a nesting pair face in the same or opposite directions at the nest, and (2) does the presence of extra-pair conspecifics influence this orientation?

METHODS

We observed vigilance in a dispersed colony of Yellow-crowned Night-herons in a 3-ha area at the northeast end of the Rice University campus in Houston, Texas (29° 43′ 07.18″ N, 95° 23′ 45.15″ W). The habitat consisted mainly of live oaks (*Quercus virginiana*) (88%) with a small number of loblolly pine (*Pinus taeda*) (5.1%), water oak (*Q. nigra*) (3.6%), willow oak (*Q. phellos*) (1.4%), post oak (*Q. stellata*) (1.2%), yaupon (*Ilex vomitoria*) (0.3%), and Shumard oak (*Q. shumardii*) (0.3%). The herons were observed nesting only in live oaks.

We observed 86 nests on the first day of our study (1 Apr 2005). By the end of our study (20 Apr 2005) we had observed the establishment of 20 more nests for a total of 106 nests. The colony was composed of clusters of 5–10 nests spaced 5–10 m apart. Each cluster of nests was distributed over 5–6 trees with overlapping canopies, and distances between clusters of 15–30 m. During this 20-day period, in which the herons engaged in nest-building, egg laying, and incubation, we surveyed the population once between 0900 and 1100 hrs and once between 1200 and 1400 hrs CST during each observation day. It took 30–60 min to survey the entire site.

We used binoculars to locate pairs of herons either in or near their nests and recorded data only when both adults were present in their nest or on a branch within 1 m of their nest. We recorded the orientation for each pair as opposite or same to describe the directions the mated pair faced when near the nest. We classified herons as having the same orientation if they faced <90° apart or in opposite orientation if they faced ≥90° to a maximum of 180°. We also noted if an extra-pair conspecific was present within an estimated 5 m of the pair's nest and if either or both members of the pair were facing directly towards it or within ±10°. We used the statistical package JMP 5.1 for data analysis and considered differences to be significant only if $P < 0.01$ to compensate for a small amount of pseudoreplication (157 observations of 106 nests).

RESULTS

Mated pairs of Yellow-crowned Night-herons faced in opposite directions in 73% of the time (114 of 157 observations, $P < 0.0001$, $\chi^2_1 = 33.3$), and extra-pair conspecifics were present within 5 m of the pair's nest 28% of the time (44 of 157 observations). Fifty-three percent (23 of 43 observations) of same-oriented pairs had an extra-pair conspecific present whereas only 18% (21 of 114 observations) of opposite-oriented pairs had an extra-pair conspecific present. A two-way contingency analysis revealed that extra-pair conspecifics were significantly ($P < 0.0001$, $\chi^2_1 = 19.68$) more common near nests with same-oriented pairs compared to nests with opposite-oriented pairs.

At least one of the resident adults faced the extra pair bird in 42 of 44 observations ($P < 0.0001$, $\chi^2_1 = 44.73$). When both members of the mated pairs faced in the same direction and an extra-pair conspecific was present, they faced towards the conspecific in 96% of the observations (22 of 23 pairs, $P < 0.0001$, $\chi^2_1 = 23.66$). When members of the mated pair were facing in opposite directions, one member of the pair faced the extra-pair bird in 95% of the observations (20 of 21 pairs, $P < 0.0001$, $\chi^2_1 = 21.07$).

DISCUSSION

Yellow-crowned Night-herons are monogamous and nest singly or in dispersed colonies in tall trees (Watts 1995). When both pair members are present, facing in opposite direction provides a collective wider field of view. We found that nesting Yellow-crowned Night-herons faced in opposite directions significantly more often than would be expected by chance and when extra-pair conspecifics were present, pairs more commonly oriented in the same direction towards the conspecifics.

This high frequency of opposite orientation could have developed as a result of predation. Possible predators of eggs and chicks include American Crows (*Corvus brachyrhynchos*), common raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), domestic cats

(*Felis catus*), and dogs (*Canis lupus familiaris*) (Watts 1995). We observed only American Crows in the immediate vicinity of the colony, although dogs, cats, and opossums are also present in the area. American Crows elicited alarm calls that alerted other Yellow-crowned Night-herons and caused the crows to leave the area. Facing in opposite directions may facilitate crow detection.

Orientation of mated pairs could result from factors unrelated to vigilance. For example, the size and shape of each heron's body may make it easier for pairs to share a nest when facing in opposite directions. In addition, opposite orientation could be used to keep bills, the primary weapon of ardeids, away from potential mates. We consider these possibilities to be unlikely. For example, opposite orientation was observed even when a member of the pair was on a branch within 1 m of the nest. In those cases, spatial constraints and the possibility of injury would no longer limit orientation.

The colony structure of Yellow-crowned Night-herons may increase vigilance against conspecifics that could steal nesting material, participate in extra-pair copulations, kill chicks, or otherwise diminish a pairs' reproductive success. Early in the nesting season, we often observed conspecifics removing twigs from each other's nests when the occupants were not present, as has been observed by others (Nice 1929, Darden 1962, Bagley and Grau 1979). Theft of nesting material may explain the observed vigilance against conspecifics.

Vigilance of Yellow-crowned Night-herons may result from the threat of extra-pair copulation. Members of a pair in many socially monogamous bird species opportunistically copulate with extra-pair individuals (Jennions and Petrie 2000, Griffith et al. 2002). Darden (1962) described a Yellow-crowned Night-heron courtship triad in which a female performed courtship behavior with two males, then mated with one, and eventually pair-bonded with the other.

Another explanation for vigilance against extra-pair herons is depredation of chicks. Juvenile Black-crowned Night-herons (*Nycticorax nycticorax*), a closely related species, have been observed depredating chicks and adults have been observed eating Cattle Egret (*Bubulcus ibis*) chicks (Riehl 2006; D. W. Mock, pers. comm.). Yellow-crowned Night-herons may do the same.

We believe the high frequency of opposite direction orientation by Yellow-crowned Night-herons probably functions in nest vigilance.

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New Display Behavior in Male Kori Bustard (*Ardeotis kori struthiunculus*)

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ABSTRACT.—Kori Bustards (*Ardeotis kori*) are polygynous and males display singly or in loose lek formations to females during the breeding season. A new display, head tossing, has been observed on repeated occasions by five different males (all *Ardeotis kori struthiunculus*) in the Smithsonian National Zoological Park, Dallas Zoo, and San Diego Wild Animal Park. This display has not been reported for *A. k. kori* or in any other *Ardeotis* species. Trained behavior watchers recorded detailed observations of a male bustard's booming behavior and frequency in 2004 and 2005; over the 2 years they collected 407 hrs of booming data. Head tossing occurred when the male rapidly threw his head backward onto his back. The head tossing display further exposed the white neck feathers and the motion of head tossing was extremely visible. Head tossing was followed by a cessation of booming or was a transition between additional booming sessions. Head tossing primarily occurred at the end of a six-boom calling bout (90% of the time) and was observed infrequently (less than 2% of all booming bouts). Head tossing appears to occur predominantly during the early phases of the breeding cycle and may function as a territorial marker directed at other males, and potentially provides information about the rank of the displaying male. *Received 2 February 2006. Accepted 30 January 2007.*

Bustards (Otididae) are medium to large ground dwelling birds that inhabit the open plains and semi-desert regions of Africa, Australia, and Eurasia. Agricultural practices including overgrazing, hunting, trapping, habitat loss, droughts, and wars are the foremost threats facing all bustard species.

The Kori Bustard (*Ardeotis kori*) is declining throughout its range (Collar 1996). The species is large, highly dimorphic, and comprises two subspecies classified by geographic distribution, size, and plumage variations. One population, *A. k. struthiunculus*, resides in eastern Africa; the nominate race *A. k. kori* occurs in southern Africa (Collar 1996).

Kori Bustards are polygynous and males display singly or in loose lek formations to females during the breeding season. Prior to full display, males engage in partial display in which they cock their tails, partially inflate their esophagus, and strut. As full display nears, the esophagus inflates to as much as four times its normal size and resembles a balloon. This display may be seen at distances of 1 km. The male, with neck expanded, tail and wing feathers pointed downward, and crest erected, emits a low-pitched six-note booming vocalization as he snaps his bill open and shut (Astley-Maberley 1937, Hoesch 1938, Hellmich 1988).

The display of the male Kori Bustard has been described on an intermittent basis for over 100 years by many authors, but one aspect of male display has not been noted for *A. kori* or any other *Ardeotis* species. "Head tossing" has been observed on repeated occasions by five different males (all *A. k. struthiunculus*) at the Smithsonian National Zoological Park (SNZP), Dallas Zoo, and San Diego Wild Animal Park (SDWAP). This paper describes this new behavior and relates its occurrence with other display behaviors of male Kori Bustard as well as levels of testosterone and mass gain during the breeding season.

METHODS

Behavioral observations of captive Kori Bustards (*A. k. struthiunculus*) at SNZP were initiated in 1998 and continued through 2005. The flock composition at SNZP varied, comprising 1–2 wild-caught adult males, 3–4 wild-caught adult females, and one captive-born female. All birds were individually marked with colored leg bands. SH observed the birds during daily husbandry sessions inside the enclosure as well as outside the ex-

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hibit. Over 5,600 hrs of video filming were used from 1998 to 2002 to supplement personal observations by SH. Volunteer "Kori Bustard behavior watchers" observed the birds from outside the enclosure. The behavior watchers recorded detailed observations of a male bustard's booming behavior and frequency in 2004 and 2005. They collected 407 hrs of booming data (245 hrs in 2004 and 162 hrs in 2005). Display in 2004 began in late April and continued to early October (168 days). Displays in 2005 commenced in late April and ended in late August (128 days). Behavior watchers stood along the visitor-accessible side of the enclosure and noted the time of each booming series. A boom series was considered complete when a pause in booming occurred. Deviations from the normal six-boom series were also recorded. Data were collected in 1-hr shifts scheduled to represent each hour of daylight every week. No shifts were scheduled for 0700 or 1400 hrs EST, during periods when keepers were in the enclosure to feed the birds and conduct routine husbandry tasks. Data were collected March through December each year. Inclement weather during January and February did not allow for data collection. Additional observations were obtained from 1 hr of videotape from the Dallas Zoo in 1992, and from observations made by the primary Kori Bustard keeper at SDWAP.

We compared the between-year number of booming series in relation to the number of observation hours using a Chi-square goodness of fit test with the Yates correction for continuity (Zar 1999). We based expected values on the proportion of observation hours corresponding to each year, testing whether the number of booming series observed reflected the number of observation hours for each year. Similar analyses were conducted to compare the number of head tosses in relation to the between-year number of booming series and the number of observation hours.

Fecal samples already being obtained from male Kori Bustard at SNZP every 7–14 days allowed for physiological confirmation of timing of the male's breeding displays. Fecal collections ($n = 75$) occurred over a period of nearly 2 years (Jan 2004–Dec 2005). All fecal samples were placed in plastic bags, immediately frozen, and stored at −20° C until analysis.

Fecal testosterone was measured at White Oak Conservation Center, Yulee, Florida by extracting 0.5 g of feces in an aqueous buffer and assaying diluted samples with a heterologous enzyme-linked immunoassay (EIA) with a polyclonal anti-testosterone-6-carboxymethyl oxime antiserum (R156/7) and testosterone conjugate (testosterone-3-carboxymethyl oxime:horseradish peroxidase). All hormone concentrations are expressed as mass units of hormone per gram of feces.

We compared fecal testosterone levels and the SNZP male's body mass between 2004 and 2005 with *t*-tests, using JMP IN Release 4. A square root transformation (Zar 1999) was applied to testosterone levels prior to analysis.

RESULTS

Calling bouts of male Kori Bustard at SNZP usually included six booms. Only 2.93% of bouts observed contained fewer than six booms. One aspect of male display not previously noted for *A. k. struthiunculus* is head tossing. This display usually occurred at the end of a normal six-boom calling bout when the male rapidly threw his head backward onto his back (Fig. 1). The duration of the toss was no more than 1 sec and was only performed once. The head tossing display further exposed the white neck feathers and the motion of the head tossing was extremely visible. Head tossing was followed by a cessation of booming altogether or was the transition between additional booming sessions.

Head tossing at SNZP was observed infrequently and, during the behavior watch of 2004, was only observed during the first month after displaying began (Fig. 2). In 2005, it was observed primarily during the first month after the onset of displaying, but also occurred several times later in the breeding season (Fig. 2). Of 3,821 calling bouts recorded in 2004, head tossing occurred 37 times (0.97%). In 2005, 1,836 calling bouts were accompanied by head tossing 36 times (1.96%). Fewer booming series were followed by head tosses in 2004 than 2005 ($\chi^2 = 8.712$, $P < 0.005$, df = 1). The SNZP male observed in these 2 years boomed more in relation to the number of observation hours in 2004

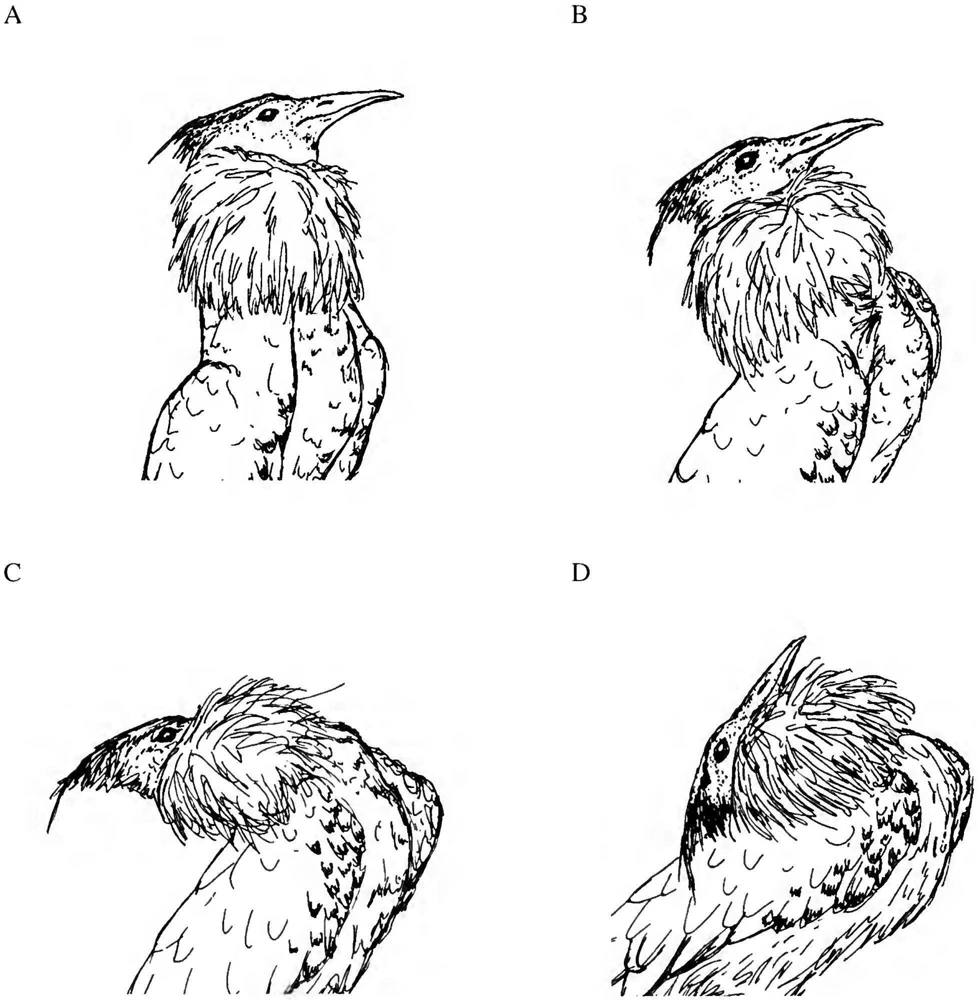

FIG. 1. Transition from booming display to head tossing display by a male Kori Bustard at the Smithsonian National Zoological Park, 2004–2005. After finishing the last call of a booming series (A), the male pulls his head towards his back (B, C) until the back of the head touches his back (D).

(mean = 15.6 bouts/hr) than in 2005 (mean = 11.3 bouts/hr) ($\chi^2 = 127.17$, $P < 0.001$, df = 1). However, the number of head tosses counted per observation hour (0.15 in 2004, 0.22 in 2005) was the same between years ($\chi^2 = 2.374$, $P > 0.10$, df = 1). Head tossing primarily occurred at the end of a six-boom calling bout (90% of the time), but was also occasionally observed after a shorter bout (7 times). Since observations at SNZP began, head tossing has been observed in three different adult male Kori Bustards. Head tossing also was confirmed in displaying males at the Dallas Zoo and SDWAP. We were unable, however, to identify the timing of the head tossing display in relation to the breeding season.

Visual observations revealed the onset of displaying for the SNZP male occurred on 25 April 2004, 10 days after an increase in testosterone levels on 15 April. In early October 2004, testosterone level decreased and display behavior ceased. Breeding displays in 2005 were first noted on 22 April, 15 days after an increase in testosterone. Testosterone began decreasing in early August 2005 and displaying was last observed on 28 August (Fig. 3). The breeding season body mass of this indi-

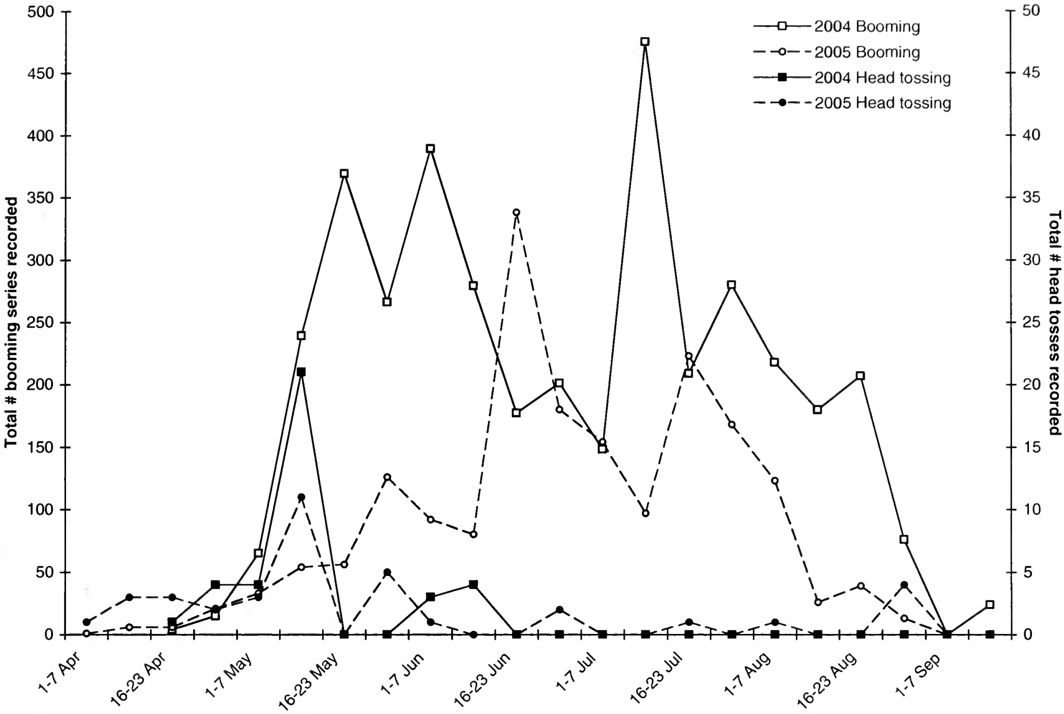

FIG. 2. Booming and head tossing frequencies by week for a male Kori Bustard at Smithsonian National Zoological Park, 2004–2005.

vidual was comparable between years (t = −1.26, P = 0.24, df = 8), but the mean concentration of fecal testosterone was lower in 2005 than 2004 (t = 2.17, P = 0.037, df = 36). Breeding season testosterone concentrations ranged from 1,102.56 pg/g to 26,491.11 pg/g in 2004, but only 276.52 pg/g to 18,355.22 pg/g in 2005.

DISCUSSION

Kori Bustards are indigenous to the grasslands and lightly wooded savannas of southern and eastern Africa. Given the open habitat where this species occurs and the solitary nature of this species, visual and auditory signals are necessary for females to find mates over long distances. The male's erection of tail and neck feathers is particularly noticeable and the booming sound can be heard for 1 km. Head tossing is a highly visual display and probably acts to increase the likelihood of a female finding a male as she approaches a lek site. The visual signals of a male's display include expansion of the esophagus, exposure of white tail feathers, and head tossing, and likely serve to attract females onto the male's mating site (Hellmich 1988); thus, they must be detectable from a great distance. Head tossing appears to occur predominantly during the early phases of the breeding cycle and may function as a territorial marker against other males, and potentially provides information about the rank of the displaying male.

Acoustic elements (e.g., booming) of male display are important because females may not be able to easily see males due to uneven terrain and vegetation (Hellmich 1988). Coupled with head tossing and an expanded esophagus, booming probably serves both to help females locate nearby males and to further attract females to breeding sites. Males at SNZP, at peak display, performed the six-note boom as many as 4–5 times in 1 min.

When a male and a female are in close proximity to one another, subtle signals (e.g., body posturing by both male and female) may serve to synchronize the birds and enable copulation (Hellmich 1988). The SNZP males increased display intensity when females came into view although this behavior has not yet

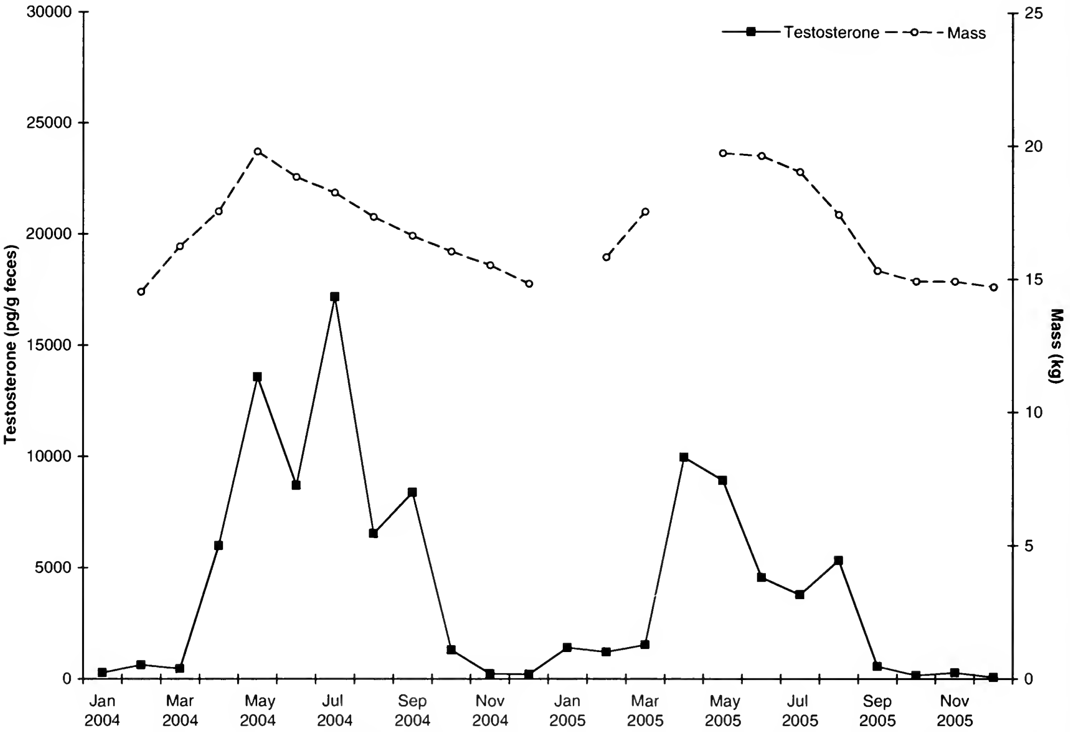

FIG. 3. Monthly changes in testosterone and body mass for a male Kori Bustard at Smithsonian National Zoological Park, 2004–2005.

been reported (Hallager 2003). Head tossing at SNZP was not observed during this final phase of courtship.

The booming pattern of the male recorded at SNZP was different in the 2 years of observation, even though peak breeding body mass (19.7 kg) was comparable between years. Fecal testosterone concentrations were lower in 2005 than in 2004 but lower testosterone levels did not impact weight gain during the breeding season. However, it is possible that reduced testosterone levels had a role in the reduced number of breeding vocalizations.

A final aspect about head tossing is its correlation with timing of neck feather molt. Males at SNZP molt their neck feathers 1–2 months prior to the onset of display. The replacement neck feathers are whiter than older feathers. Given the visual importance of the male's display in attracting females, it is likely that increased whiteness of new neck feathers enhances the visibility of the display. Molting of the white neck feathers prior to the start of the breeding season and head tossing occurring primarily at the beginning of the display season appear to be directly related.

Head tossing frequency of a second male at SNZP in 2001 was observed but not documented, and occurred during a time when two males were present together suggesting the behavior may have territorial implications. The lack of observations of head tossing in Kori Bustards is likely due to the infrequency and rapidness of the display. Observations of both subspecies in the wild are needed to supplement these findings of captive birds to further elucidate the significance and frequency of head tossing.

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Winter Prey Caching by Northern Hawk Owls in Minnesota

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ABSTRACT.—Northern Hawk Owls (*Surnia ulula*) have been reported to cache prey during the breeding season for later consumption, but detailed reports of prey caching during the non-breeding season are comparatively rare. We provided prey to four individual Northern Hawk Owls in wintering areas in northeastern Minnesota during 2001 and 2005 and observed their caching behavior. These owls cached 93% (n = 14) of prey items presented to them and consumed one item immediately after capture. A number of bird species relocate stored food by remembering the spatial locations of caches. Prominent landmarks (dead trees larger than the surrounding vegetation, sites concealed in the snow next to a utility pole or clump of grass) or sites near them were often selected for caching by Northern Hawk Owls and likely facilitate relocation of stored prey. Prey caching during winter allows exploitation of temporary increases in prey abundance and may aid in survival during times of food shortage or adverse weather. *Received 24 October 2006. Accepted 14 March 2007.*

The Northern Hawk Owl (*Surnia ulula*) is "one of the least-studied birds of North America" (Duncan and Duncan 1998:1). It resides nomadically, in response to prey availability, in boreal forests throughout its Holarctic breeding range (Andersson 1980, Mikkola 1983). In some years the species wanders well south of its year-round range during winter. These irruptive winter movements are believed to result from reproductive success in preceding years and low prey availability in the year of irruption (Duncan and Duncan 1998). Northern Hawk Owls are primarily diurnal and hunt from tree top perches (Duncan and Duncan 1998). Small mammals comprise the bulk of their diet, but birds become important during winter (Hogstad 1986, Rohner et al. 1995).

Several owl species have been reported to cache prey, particularly during the breeding season (Phelan 1977, Korpimaki 1987, Young et al. 1988). Reports of this behavior for owls during winter are rare (Collister 1995). Prey caching by Northern Hawk Owls has been observed during nesting (Ritchie 1980, Kertell 1986) and in winter (Collister 1995, Nero 1995), and may provide a safeguard for potential times of food shortage (Huhtala et al. 1987). A number of observers have witnessed

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winter prey caching by Northern Hawk Owls (Nero 1995, Duncan and Duncan 1998), but few detailed accounts are available in the literature (Collister 1995). We report observations of prey caching by wintering Northern Hawk Owls in northeastern Minnesota.

OBSERVATIONS

On 18 February 2001 we located a Northern Hawk Owl perched on top of a tree next to a gravel road in the Sax-Zim bog area northwest of Duluth, Minnesota. Habitat within the immediate area included thickets of deciduous shrubs and small trees interspersed with small openings and scattered medium-sized deciduous trees. Snow depth was approximately 20 cm. We offered the owl a recently road-killed Red Crossbill (*Loxia curvirostra*). The crossbill was placed in the middle of the road ~10 m in front of our parked car. Soon thereafter, the owl retrieved the crossbill, flew over some low vegetation, and disappeared into the shrubbery at or near ground level. The owl returned to its perch <30 sec later without the crossbill. Our view was obscured and we did not see what the owl did with the crossbill. We suspected, based on the short time the owl was out of view, that it did not consume it entirely and had cached all or a portion. On 19 February 2001 we returned to the same location and quickly relocated what we presumed to be the same Northern Hawk Owl. This time we brought along five commercially obtained dark-colored mice (*Mus musculus*). We placed a live mouse on the road and the owl immediately captured it. As with the crossbill, the owl carried the mouse into low shrubbery, at or near ground level, and returned <30 sec later without the mouse. Again, we could not see precisely what the owl did with the prey item, but we presumed it was cached. We then experienced identical results with two additional mice. We had no success observing the actual caching of prey by this individual due to the obscuring vegetation and opted to try a different Northern Hawk Owl 0.8 km distant along the same road. Habitat and snow cover were similar to the first location. The first mouse offered to this owl was held at arm's length. The mouse was captured and carried into nearby shrubbery at or near ground level. The owl returned to its perch <30 sec later without the mouse. It behaved similarly to the first Northern Hawk Owl and we again believed the prey was cached. We then offered a second mouse to this owl. The owl captured the mouse and this time we were able to see where it took the prey. The owl landed on the ground near the base of a telephone pole. With the mouse in its beak, it pushed its prey approximately 6 cm into the snow. The owl then used sideways swipes of its beak to push snow over the mouse. After caching its prey the owl returned to its perch within roughly the same amount of time as with the previous captures. This is the only instance where we observed prey being cached, but are confident the other mice and the crossbill were also cached.

We returned to northeastern Minnesota during mid-March 2005 and recorded Northern Hawk Owl prey caching behavior in more detail. Observations were made of two owls. Dead, white lab mice were frozen for transport and thawed before being offered to the owls. The first owl was west of Duluth, in Aitkin County, on the morning of 12 March 2005. Habitat within the immediate area was a mosaic of thickets (mostly small deciduous trees ~5–6 m tall), openings, and occasional medium-sized conifers and deciduous trees. Dense hardwood-conifer forest was ~0.8 km distant. A power line right-of-way paralleled the county road. Snow cover was 20–30 cm in depth. Four mice were offered to this individual. We placed the first mouse on the county road. The owl retrieved the prey and flew to a nearby telephone pole where it consumed the head before swallowing the remainder of the mouse. A second mouse was then placed on the road. The owl picked it up and took it briefly to a telephone pole. It then flew 0.16 km where it cached the mouse on top of a 2-m-high hardwood snag before returning to the capture area. A third mouse was then offered to the owl. It took this mouse 0.65 km away and cached it ~8 m above snow level in a 20-m-tall hardwood tree near the edge of the dense forest. The exact position in the tree was not observed. The owl then returned to a telephone pole near the capture site. The fourth and final mouse was presented by hand, and was taken by the owl to a pole. Briefly afterwards it flew 0.48 km and cached the mouse about 10 m above snow level (exact location not observed) in a 23-m-tall tree just inside the densely forested area. The owl then returned to a telephone pole near the capture site.

The second Northern Hawk Owl was in the Sax-Zim bog area during the afternoon of 12 March 2005 at the same location as the 2001 observations. Five dead mice were offered to this owl by hand. All were taken and subsequently cached. After each capture, the owl briefly landed on a nearby telephone pole before flying elsewhere to cache the prey. The first mouse was cached in a crevice at the top of a 3-m-tall snag, 40 m from the capture site. The second mouse was cached in snow at the base of a grass clump, 60 m from the capture site. The third mouse was cached in snow 45 m from the capture site. Caching behavior for mice cached in the snow was similar to that observed in 2001. The fourth mouse was cached in a large shrub 100 m from the capture site (details not observed). The fifth mouse was cached 6 m above snow level in a 12-m-tall snag (diameter = 22 cm at the cache site). This mouse was placed beneath loose bark with only its hind legs and tail remaining visible. Distance from the capture site was not recorded but was <200 m.

DISCUSSION

Caching behavior is exhibited by a number of bird and mammal species, and provides critical resources during times of food scarcity (Sherry and Vaccarino 1989, Sklepkovych and Montevecchi 1996, Samelius et al. 2002, Rogers 2005). This strategy seems particularly important in regions of climatic extremes. Prey caching appears to be a common behavior in wintering Northern Hawk Owls (Collister 1995, Nero 1995, Duncan and Duncan 1998). However, caching is rarely reported for non-breeding owls (Collister 1995). The four Northern Hawk Owls observed cached 93% (n = 14) of prey items presented to them. One item was eaten immediately after capture. As with other prey-caching species, the strategy of storing prey allows Northern Hawk Owls to take advantage of temporary increases in prey abundance and may aid in survival during times of food shortage or adverse weather (Collister 1995). Snow and sub-freezing temperatures can preserve prey for lengthy periods (Ehrlich et al. 1988).

Several species within the family Corvidae possess the ability to accurately recover cached food items through spatial memory (Balda and Kamil 1989, Heinrich and Pepper 1998). Our observations of winter prey caching and those of others (Collister 1995, Nero 1995, Duncan and Duncan 1998) document that Northern Hawk Owls regularly cache prey at relatively prominent visual sites, suggesting their ability to recall landmarks. These sites include dead trees larger than the surrounding vegetation, conspicuous tree cavities such as old woodpecker holes, and sites concealed in the snow next to a prominent pole, tree, or clump of grass. These visual features may facilitate recovery of stored prey.

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Willets Kleptoparasitize and Use White Ibis as "Beaters"

William E. Davis Jr.[1,3] and Jerome A. Jackson[2]

ABSTRACT.—We report observations of Willets (*Catoptrophorus semipalmatus*) using White Ibis (*Eudocimus albus*) as "beaters" to disturb prey and kleptoparasitizing (stealing) prey from them. Our observations occurred at J. N. "Ding" Darling National Wildlife Refuge on Sanibel Island, Florida on 8 December 2004. We observed these behaviors in four White Ibis-Willet pairs and describe one instance in detail and document it with photographs. To our knowledge this is the first documentation of a Willet using other birds as beaters and the first case of Willets stealing from White Ibis, although many records exist of Willets stealing from other shorebirds. We believe the use of beaters by Willets may be an under-reported foraging behavior. *Received 11 April 2006. Accepted 9 October 2006.*

Many animals follow other animals and use them as "beaters," where one species benefits by capturing prey disturbed by the beater. This behavior is common among herons (Ardeidae) (e.g., Christman 1957; Parkes and Bressler 1963; Leck 1971; Davis 1985, 2000, 2003b; Kushlan and Hancock 2005) and has been reported for sandpipers (Scolopacidae) (e.g., Davis 2003a). Interspecific kleptoparasitism (stealing food by an individual of one species from an individual of another species) is fairly common among non-passerine birds (Brockmann and Barnard 1979). It is seldom reported for sandpipers, although known for Willets (*Catoptrophorus semipalmatus*) (Lowther et al. 2001). Here we report Willets using White Ibis (*Eudocimus albus*) as beaters and a Willet stealing from an ibis at J. N. "Ding" Darling National Wildlife Refuge (DDNWR) on Sanibel Island, Florida.

OBSERVATIONS

At about 1015 hrs EST on 8 December 2004, we independently noticed single Willets foraging closely with a White Ibis on at least four occasions. In each case, the ibis was an adult (white-plumaged), the foraging pair was separated from other foraging birds by >10 m, the Willet was the follower, and the association was maintained for >15 min. The birds were foraging at low tide in the extensive (>1,000 ha) mangrove-fringed impoundment north of the Cross Dike Trail. These birds were part of an assemblage of clumped loafing and scattered feeding birds, including several hundred herons, egrets, ibis, and

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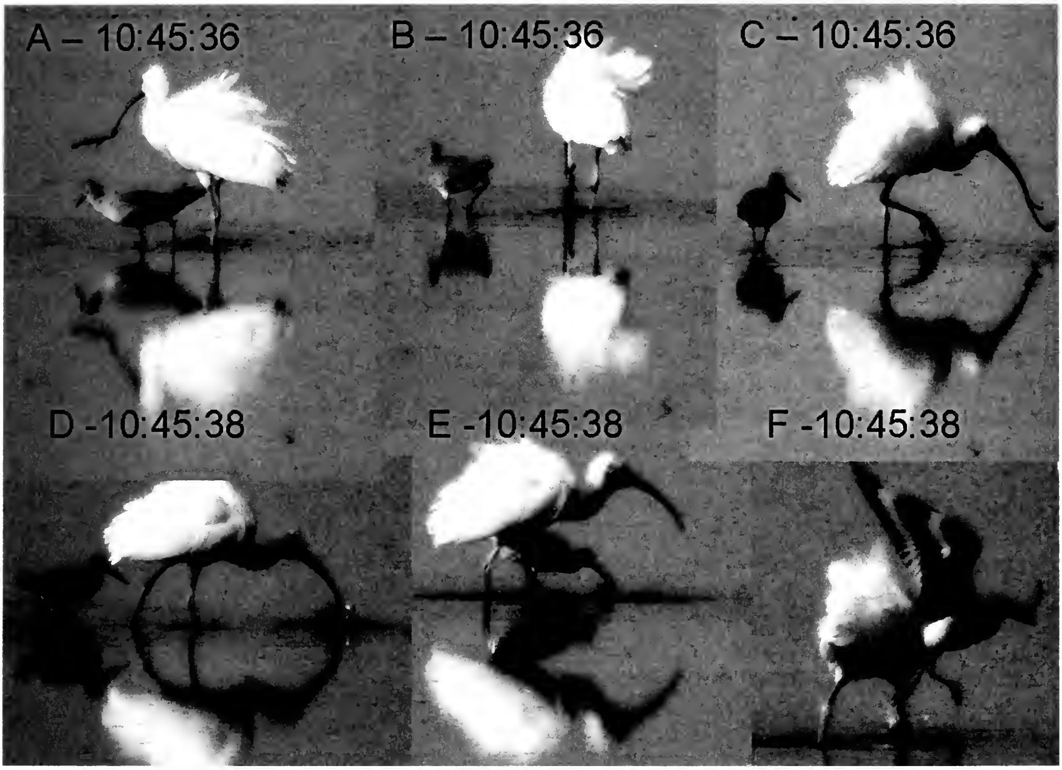

FIG. 1. Sequence of six consecutive photos — the last 3 sec of a 20-sec bout during which a White Ibis captured what appeared to be a polychaete worm and a Willet followed the ibis through four consecutive 360-degree turns as the ibis tried to protect its prey. In frame A, the ibis had been in possession of the worm for about 17 sec and had turned in place through three 360-degree turns. On the fourth turn the Willet grabbed the polychaete in frame E and the ibis lunged at the Willet as it fled with the worm in Frame F. Photographs by J. A. Jackson using a Nikon D-1X camera and 400 mm lens at 3 frames/sec.

shorebirds. Each Willet-White Ibis pair was foraging in 7–12 cm deep water. Each ibis probed the mud while the Willet visually searched for food within about a meter of the ibis while being noticeably observant of the success or potential success of the beater ibis. When an ibis seemed to have found or captured food, the associated Willet quickly approached to within grabbing distance of the ibis's bill, whereby the ibis generally responded by turning away from the Willet. Much of the time each Willet followed its beater, changing directions with the ibis, and darting to strike at prey items stirred up by the tactilely foraging ibis.

We began systematic observations of one Willet-White Ibis pair at 1028 hrs. The Willet followed the ibis through four turns in a zigzag pattern, establishing that the Willet was following the ibis. At 1031 hrs the Willet walked about 12 m and chased an approaching Willet, and then flew back to the ibis. The Willet chased another Willet at 1033 hrs and returned to the ibis at 1035 hrs. At 1036 hrs the ibis caught a probable polychaete worm and shook it, dropping a large piece of the prey that the Willet immediately picked up. The Willet stayed within a meter of the ibis, often moving close to the ibis's bill, and made a number of strikes at prey presumably stirred up by the ibis. At 1037 hrs the Willet again walked towards an approaching Willet and then returned to the ibis. At 1040 hrs the ibis stopped foraging and stood without moving. The Willet wandered ~20 m away but returned when the ibis resumed foraging at 1045 hrs. The ibis caught another polychaete, about 12 cm in length. The Willet quickly attempted to take the worm from the ibis but the ibis responded by turning away. In a 20-sec bout captured in photographs the Willet chased the ibis through four 360-degree turns, finally grabbed part or all of the worm from the ibis, and flew about 2 m as the ibis attempted to retrieve its prey (Fig. 1). We ended our observations at 1052 hrs.

DISCUSSION

We have found no reference to Willets using other birds as beaters; however, Willets are known to steal from other shorebirds. Willets stole food items from Long-billed Curlews (*Numenius americanus*; Stenzel et al. 1976; L. Tibbitts cited in Lowther et al. 2001); in California, Willets attempted to steal prey from a variety of shorebird species (G. W. Page cited in Lowther et al. 2001). Sanderlings (*Calidris alba*) have been observed using Ruddy Turnstones (*Arenaria interpres*) as beaters in Florida (Davis 2003a). Both White Ibis and Ruddy Turnstones "disturb" their local environment in efforts to find prey, the ibis by probing and turnstones by turning over debris. Kleptoparasites are opportunists that search for visible prey, whereas the White Ibis and Ruddy Turnstone are creators of opportunity. Our observations of at least four Willets, separated by up to 100 m, using White Ibis as beaters suggests use of beaters by Willets may be at least locally common, may be under-reported, and suggests that more observations are needed. Brockmann and Barnard (1979) suggest feeding associations based on beaters may lead to prey stealing. We agree and suggest the close following of ibis by Willets likely led directly to kleptoparasitism by Willets observed in this study. Willets defend feeding territories in both breeding and winter seasons (Lowther et al. 2001 and references therein); defending the ibis beater from other Willets is consistent with the species' territorial behavior.

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Observation of a Northern Cardinal Nest Reused by a Gray Catbird in the Same Season

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ABSTRACT.—We report a Gray Catbird (*Dumetella carolinensis*) reusing a Northern Cardinal (*Cardinalis cardinalis*) nest in the same breeding season. The Northern Cardinal nest failed during incubation on 19 June 2006, but the Gray Catbird nest was successful, fledging three young on 31 July 2006. Nest site availability does not appear to be the reason for reuse of the nest. Time constraints late in the breeding season may result in use of old nests. *Received 21 September 2006. Accepted 11 January 2007.*

Reuse of the same nest is well documented among colonial breeders (Shields 1984), cavity nesters (Harvey et al. 1979, Newton 1994), and species nesting on natural ledges and artificial structures (Bent 1942). Presumably, these birds reuse nests due to scarcity of suitable nest sites. A few non-colonial nesting passerines have been documented reusing nests from 1 year to the next (Marshall et al. 2001). There have been few records of a passerine reusing the nest of a different passerine in the same breeding season. One instance involved a Gray Catbird (*Dumetella carolinensis*) usurping a Brown Thrasher (*Toxostoma rufum*) nest in its territory (Nickell 1965). A non-passerine, the Mourning Dove (*Zenaida macroura*) is an example of a species that has been reported reusing nests in the same season (Mirarchi and Baskett 1994).

There are at least two reasons why birds may not reuse nests in the same breeding season. One is old nests may have a greater number of parasites from previous nesting attempts (Rendell and Verbeek 1996). Also, if a nest was depredated the predator may be more likely to depredate a nest it has already located. There are at least two reasons why birds would benefit from reuse of an old nest in the same season. One, the number of nest sites may be limited (Curson et al. 1996). Second, nest reuse may be a strategy to reduce the amount of time and energy spent building nests (Curson et al. 1996).

STUDY AREA AND METHODS

Nest searching was conducted in forest plots on the University of Illinois South Farms Agricultural Research Complex (40° 04′ N, 88° 13′ S) as part of an ongoing study on passerine birds. Several species were found nesting, including Northern Cardinal (*Cardinalis cardinalis*) and Gray Catbird. Nests were checked every 3 days until the nest fledged or failed.

RESULTS

On 8 June 2006 a female Northern Cardinal was observed building a nest in a black cherry (*Prunus serotina*) tree, 2.1 m above ground level. The Northern Cardinal had laid one egg on the first nest check after it was found, was parasitized by a Brown-headed Cowbird (*Molothrus ater*) on the second check (one Northern Cardinal egg and one Brown-headed Cowbird egg), and was depredated by the following check on 19 June 2006. On 24 July 2006 the same nest was observed being used by Gray Catbirds. Some sticks had been added to the outside. It had three nestlings approximately 5 days of age. All three nestlings fledged successfully on 31 July 2006.

Gray Catbirds incubate eggs for approximately 13 days, which would indicate the nest was active by 7 July 2006. The Northern Cardinal nest would have been inactive for about 3 weeks before the Gray Catbirds began using it. The male Gray Catbird was banded previously and was an after-second year (ASY) individual. Previously, in the same year, it had

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nested 150 m north of the site successfully with an unbanded female. That nest fledged three young on 16 June 2006. The females at both nests were unbanded and may have been the same individual.

DISCUSSION

It is unknown why open cup nesting passerines do not reuse nests. There are several different theories. Nest parasites can reduce the number and condition of young that fledge from a nest. Nest depredation and brood parasitism may increase if the previous nest attempt was unsuccessful. Gray Catbird brood parasitism from Brown-headed Cowbirds is not an issue, given they eject cowbird eggs from their nest (Rothstein 1975). Reuse of another species' nest may also be limited by a species' preference for certain nest building materials or nest structure. Additionally, old nests may not be structurally sound.

The scarcity of nest reuse is also puzzling given the potential benefits to reusing a nest. A study of Great Tits (*Parus major*) showed the earlier the young fledged, the greater the survival rate (Naef-Danzer et al. 2001). The few days an adult saves using an old nest may be valuable in development of the young prior to migration. Reusing old nests would also decrease energy demands on the parents, because they would not need to build a nest.

It is reasonable this nest was reused by Gray Catbirds to raise one more brood. We believe the reason the Gray Catbirds reused the nest, rather than build a new nest, was due to time constraints. The average departure date for Gray Catbirds in central Illinois is 15 September (Bohlen 1989). Gray Catbirds incubate for 13 days and feed young for up to 24 days (Baicich and Harrison 1997). Thus, they would need to begin nesting approximately no later than the first of August to raise their young to independence. Our findings are consistent with Cavitt et al. (1999), that Gray Catbirds may reuse nests as a time saving mechanism.

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Aerial Predation of a Bat by an American Crow

Daniel L. Hernández,[1,3,4] Jared J. Mell,[1] and Muir D. Eaton[2]

ABSTRACT.—We report predation by an American Crow (*Corvus brachyrhynchos*) of a bat in flight. We observed an aerial attack of a little brown bat (*Myotis lucifugus*) by a crow, followed by consumption of the prey item. American Crows are reported to have a wide variety of foraging strategies and food items; consumption of bats, in general, has not been reported among them. *Received 14 April 2006. Accepted 9 October 2006.*

American Crows (*Corvus brachyrhynchos*) are known to be omnivorous, consuming a wide range of plant and animal prey, including carrion. Although plant material usually comprises the majority of stomach contents, invertebrates, eggs, and small vertebrates, including birds, are common food items for crows (Verbeek and Caffrey 2002). Of the small vertebrates recorded in crow diets, amphibians, reptiles, and small rodents predominate (Hering 1934, Young 1989, Verbeek and Caffrey 2002). Much of crow foraging occurs by searching on the ground or scanning from a perch (Verbeek and Caffrey 2002). However, they have been observed using a variety of foraging strategies from fishing (Hulse and Atkeson 1953) to catching prey from the air (Clark 1914, Putnam 1992). Crows can be industrious in capture of large numbers of prey (George and Kimmel 1977), and caching behavior is common (Verbeek and Caffrey 2002).

OBSERVATIONS

At approximately 1330 hrs CDT, two of the authors (DLH and JJM) witnessed an American Crow attack and eat a little brown bat (*Myotis lucifugus*) on the campus of St. Olaf College in Northfield, Minnesota (Rice County). The bat was first observed flying near a campus building (Buntrock Commons) when a crow made several dives toward the bat in flight. The crow did not contact the bat on the first two attempts. However, on the third attempt, the crow hit the bat, knocking it to the ground. The attack occurred ~20 m from the authors view, and it was not clear whether the crow used its beak or talons to attack the bat. The crow descended upon its prey, but the authors flushed the crow in an attempt to collect the bat. The bat lay motionless on the ground for several seconds, allowing the authors to positively identify it as *M. lucifugus*. During this time the crow remained perched on a tree branch at a distance of ~5 m in clear view of the bat. The bat resumed flight before the authors could capture it. Once airborne, the bat was immediately chased by three crows, one of which was the initial attacker. The other two crows were not in close proximity to the initial attacker when the second pursuit began. The bat was knocked from the air and followed to the ground by one of the crows. It was not clear whether or not this crow was the initial attacker. The crow began to eat the bat, and a second attempt to flush the crow from its prey failed. The crow took the bat in its beak and flew to a tree ~10 m from the capture site where it continued to feed on the carcass.

DISCUSSION

Accounts of predation on bats by birds have been noted previously (Gillette and Kimbrough 1970), including predation by other corvids (Allan 1947, Elwell 1962). Both of these notes report attacks by a Blue Jay (*Cyanocitta cristata*) on a bat carrying young in an attempt to take the juvenile bat from the mother and in neither case was the adult bat killed. Rosevear (1965) reports finding bat re-

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mains in the stomach contents of a corvid in Africa. However, it is not clear whether this was the result of predation by the bird or if the bat was a scavenged food item. Our observations of the capture of a bat on the wing may not seem surprising, given the varied diet and feeding strategies of crows. However, this is the first such observation recorded, as far as we know, and bats are not a reported food item for American Crow.

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A January Specimen of the Flammulated Owl from Northern New Mexico

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ABSTRACT.—I report the first mid-winter specimen of a Flammulated Owl (*Otus flammeolus*) from within the USA breeding range of the species, an adult male found freshly dead on 2 January 1996 at Santa Fe, New Mexico following the season's first snowstorm. This event, plus an additional specimen found dead in late autumn within the New Mexico breeding range, supports the argument this species appears unable to successfully overwinter in its USA breeding range. *Received 17 November 2006. Accepted 8 September 2007.*

The Flammulated Owl (*Otus flammeolus*) is a small, insectivorous species typical of montane pine (*Pinus*) forests of western North America. It is generally recognized as strongly migratory, but its migration patterns are poorly understood (McCallum 1994). Experimental and other evidence suggest this owl cannot withstand low temperatures nor enter torpor (e.g., Banks 1964, Ligon 1968, Winter 1974). There has been disagreement as to whether the species may be able to winter within its USA breeding range, including whether it may take vertebrate prey to do so (Holt 1996, McCallum 1996). In this note, I present the details of a Flammulated Owl found dead in mid-winter within the species' breeding range in northern New Mexico. I also present details of another Flammulated Owl found dead under similar circumstances in late autumn and discuss these events regarding this owl's potential to overwinter within its breeding range north of Mexico. The New Mexico specimens reported here are in the collection of the Museum of Southwestern Biology (MSB) at the University of New Mexico.

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OBSERVATIONS

Following an unusually warm autumn and early winter, the city of Santa Fe and the surrounding mountains of northern New Mexico received the season's first snowstorm on the afternoon and evening of 1 January 1996; the storm sharply reduced temperatures and blanketed the region under heavy snow. On the morning of 2 January, the groundskeeper of a local inn discovered a small owl, freshly dead, near the building's entrance. J. L. Herring of the New Mexico Department of Game and Fish retrieved the owl that day and placed it in a freezer. The owl was delivered to me on 2 February, whereupon I recognized it as a Flammulated Owl. The owl was again frozen until 19 October 1996 when it was prepared as a study skin by D. C. Schmitt.

The specimen (MSB 23307) is an adult male. It had no body fat or any body cavity fat, suggesting that it was not in condition to migrate; the mass when prepared was 35.8 g, considerably below the 53.9 g mean reported for adult males (McCallum 1994). No molt was evident. The stomach was filled with insect parts. These stomach contents were preserved and identified by S. L. Brantley as being parts of earwigs (*Forficula auricularis*), ground beetles (Carabidae), and darkling beetles (Tenebrionidae), indicating the owl probably had been recently foraging on the ground, likely in moist litter. The testes measured 5 × 3 mm, unusually large for the nonbreeding season (R. W. Dickerman, pers. comm.). No skull hemorrhaging or other trauma was evident, suggesting the owl died not from injury but from cold. The specimen is grayish (not reddish) and heavily (not faintly) marked, typical of the local breeding birds of the Great Basin and Southern Rocky Mountains, i.e., *O. f. frontalis* Hekstra (Marshall 1997).

DISCUSSION

There are few winter Flammulated Owl specimens for the United States and none from within the owl's breeding distribution (Collins et al. 1986, McCallum 1994); the few winter observations from breeding habitat were questioned by McCallum (1994, 1996). The three mid-winter specimens previously reported were from outside the breeding range or were at elevations lower than breeding habitat: 2 January in Louisiana (Glasgow et al. 1950), 18 January in California (Stephens 1902), and 16 February in Arizona (Simpson and Werner 1958). The dead owl was found at 2,015 m, well within the species' breeding elevation range, and the inn (35° 38′ 24″ N, 106° 00′ 55″ W) is only 5.7 km southwest of the Santa Fe Indian School where Jensen (1923) reported Flammulated Owls breeding over a period of several years. The eastern portions of Santa Fe extend into the Sangre de Cristo Mountains where the species breeds commonly.

I suspect this owl, whether a local breeder or a migrant from elsewhere, remained in or near breeding habitat until it encountered sudden cold and heavy snow cover. November and December 1995 were exceptionally warm in northern New Mexico—average temperatures for those months in north-central New Mexico were, respectively, 10.9 and 11.2% above the previous 100-year (1895–1994) monthly averages (National Climatic Data Center 2006). The major snowstorm on 1 January 1996 abruptly ended those mild conditions. The owl appears to have survived into January by ground foraging for insects, but this diet apparently was insufficient to maintain normal weight and the bird quickly succumbed to the sudden onset of markedly cold temperatures.

Flammulated Owls typically migrate from New Mexico by mid-October (e.g., DeLong 2006). Recently, however, additional specimens of late-lingering Flammulated Owls have been obtained, including the first certain November records for the state. One of these, an adult female (MSB 25294) found freshly dead by P. S. West at Bitter Lake National Wildlife Refuge, Chaves County on 20 November 2005, was far from suitable habitat and was presumably a late migrant; it had no fat, a mass of 41.9 g, and its nearly empty stomach contained parts of only two individual ground beetles (*Cymindis* spp.); the specimen is grayish but not heavily barred, complicating subspecies identification. The other owl, an adult female (MSB 24543) salvaged by M. L. Watson at the village of Cochiti Lake, Sandoval County on 28 November 2004, was found freshly dead at the base of a ponderosa pine (*Pinus ponderosa*) following the first major snowfall of that season; the specimen, grayish and heavily barred as in the local subspecies, had little fat but was not emaciated. However, mass was not recorded and stomach contents were not saved. Cochiti Lake village, at an elevation of 1,735 m in the foothills of the Jemez Mountains, is immediately adjacent to breeding range of the species. Finding of the Cochiti and Santa Fe owls closely following onset of severe winter weather supports the contention this species appears unable to successfully overwinter within its breeding habitat in North America north of Mexico, at least under the present climatic regime.

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Once Upon a Time in American Ornithology

Extinction: the Passenger Pigeon, Last Hopes, Letting Go

Jerome A. Jackson[1,3] and Bette J. S. Jackson[2]

"Extinct," the English word, has its origin from the Latin verb *exstinguere* . . . which originally referred to things like putting out a fire. It wasn't until 1581 that we find it used in English in the sense of the consequences of the death of the last male in a family line—of humans (Harper 2001). Ironically, this first use of extinct with such a meaning was almost simultaneous with the discovery of the Dodo (*Raphus cuculatus*) on the island of Mauritius in the Indian Ocean. Less than a century later the last Dodo was apparently dead, the species a victim of human exploitation for food (although they were at times reported as disgusting in taste) and predation by exotic species introduced by humans (Staub 1996). However, recognition that the Dodo was extinct took more than a century; its demise was not recognized, not comprehended, nor of little initial interest to scientists, although ultimately it came to be an icon for the biological concept of extinction. The year 1600 and the Dodo are often used as benchmarks for the beginning of an era of a dramatically increasing rate of extinction directly or indirectly caused by humans.

Among learned naturalists of the late 18th and early 19th century such as Thomas Jefferson, the concept of extinction was foreign and not believed. Jefferson's (1853:55) view in 1787 was that: "Such is the economy of nature, that no instance can be produced of her having permitted any one race of her animals to become extinct; of her having formed any link in her great work so weak as to be broken."

The Baron Georges Cuvier (1799) had recognized animal extinction through his work with fossils. By the 1860s and publication of Charles Darwin's *Origin of Species*, the concept was generally recognized and the finality of extinction of species understood. It was also understood that: (1) extinction is a natural process that is positive, linked with the continued fine-tuning of life to changing environments; (2) it is a negative process in which species unable to adapt to changing conditions are forever lost; and (3) humans were having significant roles in enhancing the rate of extinction for some species.

During the first half of the 19th century, the Great Auk (*Pinguinus impennis*) disappeared forever, the result of overexploitation by humans (Montevecchi and Kirk 1996). The Labrador Duck (*Camptorhynchus labradorius*) followed a few decades later, also almost certainly a result of human impacts (Chilton 1997). By the early 20th century more North American birds, including the Passenger Pigeon (*Ectopistes migratorius*), Carolina Parakeet (*Conuropsis carolinensis*), and Heath Hen (*Tympanuchus cupido cupido*) were gone and the Ivory-billed Woodpecker (*Campephilus principalis*), Whooping Crane (*Grus americana*), and others seemed sure to follow.

With each species there have been speculations as to the cause of loss and, ultimately, links to human actions. For each there has also been a level of disbelief in human involvement in the loss or that the loss has even occurred. The recognition of the probability of extinction, responses to the threat of extinction, the debate over its causes, and the acceptance of extinction are lengthy processes. Humanity has had a hard time waking up to the prospect of extinction. We have been late, slow, and usually ineffective in our efforts to prevent extinction, although human actions have increasingly contributed to extinction. We have also often had a hard time letting go,

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at least of charismatic species. We cling to the hope that somewhere, safe from the intrusions of humans, a small population still hangs on, waiting to be saved.

Such recognition, as epitomized by the Great Auk, initially had the negative effect of stimulating competition to secure specimens for personal and institutional collections. This at times resulted in either high monetary or institutional prestige values for specimens, thus hastening species' demise.

The pathway to extinction differs for each species, but there are also common threads. We have learned from some of these, and our conservation ethic and abilities have grown. Beginning in the early 20th century, conservation efforts were initiated as we recognized declines in bird populations linked to massive habitat loss, the millinery trade, and overhunting. These efforts, although too late and too little for some species, included dramatic increases in conservation education at all levels, increased conservation legislation, better enforcement of conservation laws, and increased interest in sport-birding.

Birding has become such a major pastime that birders are an economically significant group with established political power as well as influence by example. For many, birding has become a competitive sport with rules (Big Day criteria, etc.), scores (numbers of species seen per unit time or place), and referees (records committees), giving them some of the trappings of other sports . . . and also a semblance of the trappings of science. Add to these trappings the considerable number of citizen-science programs, and birding blends with science. Birders thereby have achieved a measure of "scientific clout," and have contributed to our scientific understanding of birds and increased the economic value of all birds, especially rare species.

The Wilson Ornithological Society has *always* fostered the link between scientific ornithology and avocational ornithology. We believe the evolution of this shared intense focus on birds by birders and scientific ornithologists has contributed to our knowledge and understanding of the loss of bird species. It has also contributed to the current debate over the possible continued existence of the Ivory-billed Woodpecker. We see links and parallels between the history of the extinction of the Passenger Pigeon and our current angst over the possible continued existence of the Ivory-bill. In the paragraphs that follow we discuss the extinction of the Passenger Pigeon as a case history and offer insight based on a broader look at the human social and political context of its demise.

John James Audubon (Audubon and Chevalier 1844: 30), in the text to accompany his *Birds of North America*, joined Alexander Wilson (1813) in describing the immensity of Passenger Pigeon flocks—as well as the devastation of their numbers brought about by market hunting and abuses such as their use for target practice and even as food for hogs. Audubon seemed aghast at the magnitude of the killing, but noted "Persons unacquainted with these birds might naturally conclude that such dreadful havoc would soon put an end to the species. But I have satisfied myself, by long observation, that nothing but the gradual diminution of our forests can accomplish their decrease, as they not unfrequently quadruple their numbers yearly, and always at least double it."

Audubon also spoke of the Passenger Pigeon's reliance on places with abundant food: beech (*Fagus grandifolia*) nuts, acorns (*Quercus* spp.), chestnuts (*Castanea dentata*), other seeds, and diverse fruits. And he further suggested their dependence on expansive old growth forest: "Forest trees of great height are those in which the Pigeons form their nests. Thither countless myriads resort, and prepare to fulfill one of the great laws of nature."

Mershon (1907), Schorger (1973), and Blockstein (2002) have chronicled the demise of the Passenger Pigeon, focusing on the immensity of its flocks and their equally immense exploitation. At first there was disbelief. The enormous flocks had just gone somewhere else: "there were just as many pigeons in the west as there ever were. They say the birds have been driven from Michigan and the adjoining states partly by persecution, and partly by the destruction of the forests, and have retreated to uninhabited regions" (Brewster 1889:290). Brewster seemed to give credence to the belief they had gone to Canada, suggesting the disappearance of the Passenger Pigeon "as a bird of the United States" in the title of his assessment of their status (Brewster 1889).

Some blamed the birds themselves for their extinction: "The primary cause for the passing of the Passenger Pigeon was its own specialized habits and a long list of biological 'defects' " (Griscom 1946:215). Suggestions of causes for their extinction abounded. Many were far-fetched. For example, some believed they died in a great storm and drowned in a lake (McConnell 1908) or they died when "vast flocks were blown out to sea and perished" (Burns 1910). Others suggested they died in a forest fire (Bartsch 1917), or died of disease in the wilds of Canada (Thompson, undated).

Between 1870 and 1900 the human population of the United States nearly doubled. Midwestern and Northeastern states were undergoing rapid growth and development and, by the end of the 1870s, the virgin forests of those regions had been cut to provide wood for railroad ties, telegraph poles, homes, businesses, and fuel. Loss and fragmentation of old growth was accelerated and might alone have caused the extinction of a species that was an obligate colonial nester and preferred extensive forests of old growth trees for its nests. Add the loss of food resources when trees were cut and intense pressure from market hunters, and it might seem the Passenger Pigeon had no hope except to look elsewhere for suitable habitat. Northern forest industries also had to look elsewhere for raw materials.

Following the American Civil War nearly 50% of the land area of some southern states reverted to federal ownership. With devastation of the war and no taxes being paid on those lands, the South remained economically depressed. But the South still had vast acreages of virgin forest. In the late 1870s, Southern congressmen and the northern forest industry found a mutual solution to their different problems. A bill was passed providing for the sale of Federal forest lands in the South. The lands were purchased by northern forest industries and, between ~1880 and 1900, the South's old-growth forests were cut (Lillard 1947, Jackson 1988). Perhaps the Passenger Pigeon might have survived if southern forests had remained, but business, politics, and growth of our nation precluded this possibility.

In the face of rapidly declining numbers, there were calls to protect the Passenger Pigeon. Efforts were made, but business and political interests prevented effective conservation. Laws were passed in the 1880s to "protect" the birds in various states, but they generally did more to protect the interests of netters over shooters rather than birds over human interests and were rarely enforced (Brewster 1889). Brewster (1889:291) noted that those netting the birds for shipment to major markets have "the powerful backing of the large game dealers in cities" and that it "is not likely that any really effectual laws can be passed until the last of our Passenger Pigeons are preparing to follow the Great Auk and the American Bison [*Bison bison*]."

As the Passenger Pigeon slipped into oblivion, American ornithologists slipped into crisis mode. Rewards were offered. One of the first was for a fresh specimen to prove that the species still existed. America's new conservation conscience stirred and, although there were certainly those eager to add a specimen to personal or institutional collections, later rewards were offered for evidence of living birds. Mourning Doves (*Zenaida macroura*), their nests, and eggs, and the eggs of other species regularly came in as documentation for Passenger Pigeons, some apparently deliberately misidentified (Burns 1910).

Schorger (1973) considers the last undisputed specimen to have been collected in Pike County, Ohio on 24 March 1900. A few inadequately documented specimens and numerous sightings were reported after that. The last known living Passenger Pigeon, a captive-hatched female that had been named Martha, died 1 September 1914 at the Cincinnati Zoo. Perhaps a few Passenger Pigeons remained well into the first decade of the 20th century. Perhaps not.

Late Passenger Pigeon records were questioned because the bird could be confused with the slightly smaller, superficially similar Mourning Dove. William Brewster (1925: 309-310) noted ". . . I have often been unable to satisfy myself respecting the identity of single birds viewed at a distance, or in unfavourable lights. For a Mourning Dove seen through mist-laden atmosphere sometimes looked as big . . . and when its colour and markings could not be discerned it might easily be mistaken for one, there being really no very obvious points of difference between the two birds in respect to either general appearance or behaviour."

Schorger (1973:286) said it more succinctly: "Sight records carry interest but little weight. Persons with wide experience with the Passenger Pigeon have been deceived . . . under certain circumstances."

We add from personal experience that individuals often see what they want to see. Rare endangered species have a price on their head: seeing them not only provides a great deal of satisfaction, but a sort of currency of competency and quality as a birder, a higher "score," and sometimes even the kind of media attention bestowed on star athletes in other sports. There is nothing *wrong* with any of this and it has value, even to science. But it is not science.

The value of sight records is that they suggest possibilities. They provide the basis for hypotheses. We accept on faith records of more common species because we know the common species is there and we believe the observer is competent and conscientious. But acceptance of such records of the rarest of the rare cannot be accepted as scientific documentation. The tenets of science require more than faith and testimonials as to the competency of an observer. Documentation must be available for other scientists—both contemporary and future—to evaluate and affirm or refute.

The Passenger Pigeon is gone, a victim of the growth of our nation, excesses, bottom lines, human ignorance of the interconnections in nature, and the bird's own social behavior and accessibility to human exploitation. Many factors contributed to its demise and it would be foolish to suggest just one unless it was "humans." With rarity some found value. To be among those who last saw it provided a sense of uniqueness, accomplishment, and self-importance. We cannot judge if late observations were deliberate deception, delusion, true mistaken identity, or truly brief glimpses of the last individual of a species wandering until the last flame of Passenger Pigeon existence was extinguished.

Passenger Pigeons went from being one of the most abundant birds ever to extinction in less than a century. In contrast, Ivory-billed Woodpeckers were more restricted in their range, non-migratory, apparently locally distributed, and never abundant. Yet there are parallels in their demise and in our last minute pursuit of hope for their existence. The Ivory-bill shared and suffered the catastrophic destruction of the Passenger Pigeon's southeastern habitat. Its populations were also fragmented. Although it did not form huge flocks, its social behavior—traveling in family groups, dependence on returning to the same roost night after night, and the potential for collectors to shoot both parents if they could locate a nest—contributed to its rapid decline once populations had been isolated and the virgin forests opened and exposed to human exploitation (Jackson 2002, 2006a).

Recognition of the probability of extinction of the Ivory-bill came nearly simultaneously with the extinction of the Passenger Pigeon. By 1912 that probability was so well known that it was even told in a children's poem by Elizabeth Gordon (1912:79):

Ivory-billed Woodpecker said:
    "Dear me!
They're cutting down my family tree,
Where can I live, I'd like to know,
If men will spoil the forest so."

By the early 1920s many believed the Ivory-billed Woodpecker could be extinct, but in 1924 in Florida and 1932 in Louisiana, permits were issued to allow Ivory-billed Woodpeckers to be collected (Jackson 2006a). Although only one breeding population was known in the 1930s, forest cutting for commerce and in the name of national defense could not be stopped. With the end of World War II, birders and scientists once again focused concern on the Ivory-bill. The Ivory-bill's possible existence as one of the rarest of the rare made it an obsession for some—fed by reports of sightings in Florida, Texas, South Carolina, Louisiana, or Mississippi at about 10-year intervals. Scientists took note, interviewed observers, and evaluated habitats. But the searching was primarily by birders. Evidence presented included inconclusive poor-quality photographs and sound recordings, and an Ivory-bill feather that may or may not have come from a living bird, but most evidence was merely observation. Some reports sounded promising and there were testimonials as to the integrity and abilities of observers. There were "believers" and skeptics.

This is the crux of the debate over the reported "confirmation" of Ivory-billed Woodpeckers in eastern Arkansas (Fitzpatrick et al. 2005) and reports of their possible existence in the Choctawhatchee River forests of north Florida (Hill et al. 2006). In April 2005, the world had awakened to the news the Ivory-bill had been rediscovered in Arkansas. For a year its possible existence had been known, but as planned for the Passenger Pigeon, the information had been kept secret as searches intensified. Conversely, Hill and his colleagues quickly made their observations public in an effort to obtain the documentation needed for confirmation (Hill et al. 2006, Hill 2007).

Sight records and controversial and inconclusive feeding sign, large cavities, videos, and audio recordings have presented us with the hypothesis that, in spite of there being more than 60 years since the species was last scientifically documented (Jackson 2002; 2006a, 2006b), it might have survived into the 21st century. The potential for confusion with a similar but slightly smaller species, the Pileated Woodpecker (*Dryocopus pileatus*), and shared habitat needs, behavior, and ecology, complicate interpretation of such evidence, just as the potential of confusing the Mourning Dove with the Passenger Pigeon. Rewards have been offered (Anonymous 2006, Jackson 2006a), but the lack of truly confirming evidence, in view of these and the magnitude of search efforts and sophistication of photographic and sound equipment used, make the Ivory-bill's presence increasingly unlikely.

Because of the nature of its habitat and potential ability to move great distances, we will never be able to chronicle the day of the Ivory-bill's demise. A declaration of extinction at this time can only be a political decision, not a scientific one. A declaration of confirmation of the Ivory-bill's survival must be a scientific one, not a political one.

The odds are long, the mountain steep, and the terrain rugged. Of course it is the "mountain" of evidence and the cut of time against the continued existence of the Ivory-bill and the "rugged terrain" of popular and scientific opinion that must be negotiated (e.g., Jackson 2006b, Sibley et al. 2006, Stokstad 2007), as well as the inhospitable habitat that the Ivory-bill last favored. We have come to terms with the reality of the extinction of the Dodo, Great Auk, Labrador Duck, Passenger Pigeon, and Carolina Parakeet. At least most of us have done so. But dreams of Ivory-bills and fires of hope burn bright in the minds of many. We seem to thrive on such dreams and hopes. It's tough to let go; it's so difficult to be sure that a species is extinct. For now, we have hope that the Ivory-bill lives, but the truth is still out there.

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BIRD LOVERS:
WILLIAM ALDEN KLAMM AND NANCY AGNES KLAMM

JEROME A. JACKSON[1]

William A. Klamm was born in 1916 in Lakewood, Ohio. He graduated from Case Western Reserve University in Cleveland in 1940 with a degree in Chemical Engineering. During World War II he enlisted in the Army Air Corps and served for 4 years, rising to the rank of Captain and commander of a fleet of bombers based in Alaska. After leaving the military, Bill spent most of his career working for a subsidiary of Pennzoil (Segall 1998).

Nancy Klamm, the daughter of William and Grace Campbell, was born Agnes Campbell in 1911 in Woodville, Pennsylvania. She graduated from Pennsylvania College for Women (now Chatham College) in 1932 with a major in chemistry and a minor in mathematics. After graduation Nancy obtained a job as a senior buyer in the Chemistry Department at Case Western Reserve University. It was there that she met William A. Klamm and they began dating. When Bill returned from the war, Bill and Nancy renewed their courtship—which included a great deal of birding. They were married on 9 September 1950 (Baranick 2002, Renkert 2002).

Bill and Nancy Klamm, approximately 1973. Photograph courtesy of Richard and Nancy Renkert.

Bill was a lifelong birder who joined the Wilson Ornithological Society in 1957. He and Nancy were very active with the Kirtland Bird Club and the Cleveland Museum of Natural History. They regularly contributed their records and short notes to the Cleveland Bird Calendar (e.g., Flannigan et al. 1974; N. Klamm 1968; W. A. Klamm 1968, 1974; W. Klamm and N. Klamm 1968), a local journal of birds and birding published by the Cleveland Museum of Natural History and the Kirtland Bird Club. Bill also published notes in the *Ohio Cardinal* (W. A. Klamm 1980–1981, 1990). The published records of Bill and Nancy Klamm in the Cleveland Bird Calendar are numerous and often simply labeled "Klamm"—Bill and Nancy were inseparable—their observations almost always made together. Both were also long-time members of the Audubon Society of Greater Cleveland.

Bill and Nancy attended their first Wilson meeting in 1958 in West Virginia and missed no meetings in the next 33 years. Bill was an incredibly meticulous, methodical record keeper, regularly writing a summary of the weather for the Cleveland Bird Calendar. He was also an avid photographer, documenting local rarities with home movies. Bill and Nancy knew birds well and the value of bird records of all sorts. They were much more than listers. They were true bird "watchers." Above all Bill and Nancy recognized the importance of ornithological research and education, and were especially supportive of student efforts, seeking out student papers to attend at Wilson meetings and later seeking out the students to discuss their presentation. In 1967 Bill gave a paper at the Wilson meeting in Crawford Notch, New Hampshire, on "Some observations on competition between Lewis' Woodpeckers and Red-shafted Flickers."

In 1968 Bill Klamm was elected treasurer

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of the Wilson Ornithological Society; he served in that capacity until 1973. I was elected to take his place as treasurer and Bill worked closely with me for most of the year. He was a wonderful mentor and he and Nancy remained my close friends. They helped a great deal when we hosted the Wilson meeting at Mississippi State University.

Nancy Klamm was never a member of the Wilson Ornithological Society except vicariously through her husband, although she too never missed a Wilson meeting in 33 years. She was an avid birder, contributor to the Cleveland Bird Calendar, and ardent supporter of local conservation efforts.

William A. Klamm died on 6 May 1998 of complications from emphysema. Following his death, Nancy sold Bill's very valuable stamp collection and donated the proceeds to the Cleveland Museum of Natural History and the Kirtland Bird Club. The funds were used to set up a lecture series in Bill's name. In April 2002 I was honored to be the first William A. Klamm memorial lecturer at the museum. Before the lecture Nancy and I had dinner together and we reminisced about Wilson meetings and field trips we had shared. She told me that she and Bill had no children and no close relatives, but had been frugal and saved a good deal of money. She was ill and knew her time was short. Nancy and Bill had discussed what they might do with their savings and Bill wanted to leave a good portion of it to the Wilson Ornithological Society. They had both decided that they wanted the money to be used as an endowment to encourage and enable students to attend annual meetings and to encourage service to the Society. They wanted only the interest to be used so that there would always be funds available. Nancy asked my opinion of their priorities. I assured her they were wonderful. Wilson meetings were a highlight of the year for Bill and Nancy. They loved the meetings and were especially interested in seeing greater attendance and participation by students.

Although an active chemical engineer by profession, birds were Bill's passion and he and Nancy birded on all seven continents. Bill was very grateful for being welcomed into the Wilson Ornithological Society and being given the opportunity to serve the Society as treasurer. It was especially fitting that the editor of *The Wilson Bulletin* who served when Bill was treasurer—George A. Hall, also a chemist by profession—was the recipient of the first William and Nancy Klamm Service Award from the Wilson Ornithological Society.

Nancy Klamm died 22 July 2002. She left 40% of her estate, about $1.2 million, to the Wilson Ornithological Society. The bequest more than doubled the Wilson Society's assets when it was received in 2004 (Morris 2003, 2004). Other bequests established the William and Nancy Klamm Endowed Chair of Ornithology at the Cleveland Museum of Natural History, renovated bird exhibits at the museum, and supported other birding organizations in the region.

Cleveland Plain Dealer reporter James McCarty, in a 1993 article describing the tenacity and enthusiasm of birders, focused on Bill and Nancy Klamm who had been birding together for 40 years (McCarty 1993: 10):

> "Now that they're retired, the Lakewood couple can be found most days at traditional birding haunts along Lake Erie, he with a video camera for chance meetings with rare birds, she doting over him, offering a sandwich from a paper bag or dabbing wind tears from his eyes with a handkerchief."

The title of the article began appropriately with "Bird lovers . . . "

They were.

ACKNOWLEDGMENTS

I thank Tom Leiden for assistance with locating individuals who knew Bill and Nancy Klamm and for sharing his own knowledge of the Klamms, and for comments on an early draft of this manuscript. Richard and Nancy Renkert, Delores Cole, Marie Graf, Ned Keller, Paula Lozano, and other members of the Kirtland Bird Club also provided valuable insights.

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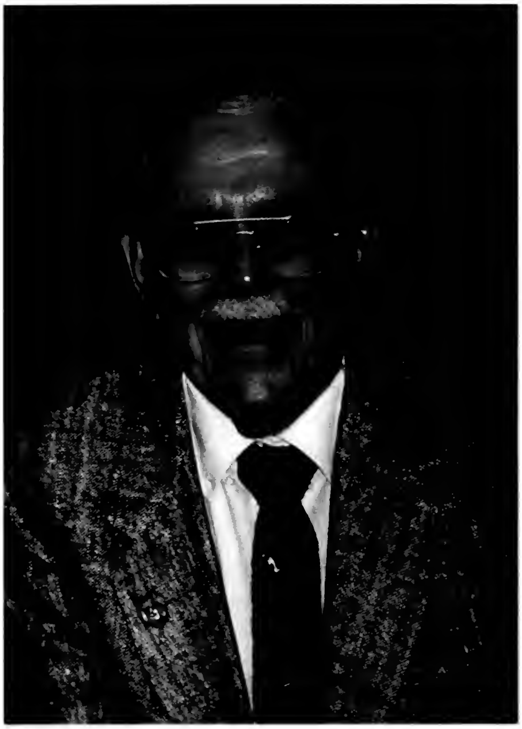
The 2007 William and Nancy Klamm Service Award



George A. Hall. 2000. Photograph by Jerome A. Jackson.

Many people have provided long and varied service to the Wilson Ornithological Society, and the first recipient of the William and Nancy Klamm Service Award epitomizes this dedication to the Society. Despite his vocation as a chemist, George A. Hall has served the Wilson Ornithological Society in many capacities over more than five decades. After joining the Wilson Ornithological Club in 1946, he was the Registration Chairman for the annual meeting at Madison, Wisconsin in 1949. He co-chaired the local committee for the 1958 annual meeting in Wheeling, West Virginia. From 1964 to 1973 he served as Editor of the *Wilson Bulletin*, which included William Klamm's tenure as treasurer. After a decade as editor, George was elected to the WOS Council in 1973. His term as Council member ended early when he was elected Second Vice-President in 1975. He served as Second Vice-President from 1975 to 1977, First Vice-President from 1977 to 1979, and President from 1979 to 1981. In 1984, he became the Ornithological Literature Editor for the *Wilson Bulletin*, a position he held for more than a decade.

George has been a perennial attendee at Wilson meetings; he attended thirty-five consecutive Wilson meetings from 1964 to 2001. In addition to serving on Council, over the years George provided varied support to the Society in numerous ways, serving as Chair of the Nominating Committee, Chair of the Wilson Prize Selection Committee, Chair of the Resolutions Committee, Chair of the Archives and History Committee, and even acting Secretary for one meeting. In 1988, he co-authored the history of the first one hundred years of the Wilson Ornithological Society with Jerome A. Jackson and Harold Mayfield. He also gave a presentation on Alexander Wilson during the centennial meeting in that same year.

Those of us who have served with George appreciated his mentoring of early-stage ornithologists, his knowledge of the Society and its workings, and his quick wit. It is with great admiration that the Wilson Ornithological Society awards the first William and Nancy Klamm Service Award to George A. Hall.—Sara R. Morris, Jerome A. Jackson, and W. E. Davis Jr. (Klamm Service Award Committee).

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Ornithological Literature

Compiled by Mary Gustafson

MANAGEMENT OF COWBIRDS AND THEIR HOSTS: BALANCING SCIENCE, ETHICS, AND MANDATES. Edited by Catherine P. Ortega, Jameson F. Chace, and Brian D. Peer. Ornithological Monographs 57. The American Ornithologists' Union, Washington, D.C. 2005: 114 pp. ISBN: 0-943610-63-X. $10.00 (paper).—Brood-parasitic cowbirds (*Molothrus* spp.) and the problems they cause for their hosts have been the subject of many studies, especially during the last two decades. Research has focused on the Brown-headed Cowbird (*M. ater*), since it is abundant across much of North America (the habitat of many ornithologists) and it affects the nesting success of many bird species. The effects of Brown-headed Cowbird brood parasitism on individual endangered species, such as Kirtland's Warbler (*Dendroica kirtlandii*), and on communities of neotropical migrants, particularly those in fragmented landscapes, have been of special interest. This volume of *Ornithological Monographs* resulted from a symposium on "Ecology and evolution of host-parasite interactions and cowbird management", held at the annual meeting of the American Ornithologists' Union, at Urbana, Illinois, in 2003. The overall purpose of the symposium was for researchers and managers to share their knowledge and ideas of cowbird control issues.

This volume contains seven chapters, most of which cover the effects of cowbird control (that is, removal) on nesting success and population growth of host species or on habitat factors affecting cowbird habitat use and abundance. Two papers were reviews of issues associated with cowbird control and host defenses. Three studies included at least some information on parasitism by Bronzed Cowbirds (*M. aeneus*) and Shiny Cowbirds (*M. bonariensis*). The introduction, by the editors, briefly discusses the papers and presented some conclusions concerning present knowledge gaps and future research needs.

In Chapter 1, Ortega et al. summarize the main cowbird management controversy; how much to focus on cowbird control in management of endangered or threatened species. They discuss laws protecting cowbirds and species affected by cowbirds and then criticize any proposed widespread cowbird control efforts, given other factors affecting host populations and the scattershot nature of such efforts.

In Chapter 2, Kus and Whitfield analyze the effects of cowbird control on productivity and population growth of Least Bell's Vireo (*Vireo bellii pusillus*) and Southwestern Willow Flycatcher (*Empidonax traillii extimus*) in California. An interesting point was the contrast between the responses of the two hosts: Least Bell's Vireos experienced significantly greater nesting productivity and populations grew after cowbird control began, although populations eventually leveled off, suggesting that habitat had become the limiting factor. Southwestern Willow Flycatchers showed somewhat higher productivity but their populations did not grow. Kus and Whitfield criticize the lack of criteria for ending or modifying cowbird control programs.

In Chapter 3, Kostecke et al. summarize and evaluate the success of the long-running cowbird control program on Fort Hood, Texas where the endangered Black-capped Vireo (*Vireo atricapillus*) nests in substantial numbers. Overall, Black-capped Vireo numbers and nesting success increased, but it was difficult to distinguish the effectiveness of shooting, trapping, and cattle removal. Kostecke et al. note that expense and local political situations may make effective cowbird and endangered species management more difficult.

In Chapter 4, Cruz et al. summarize the effectiveness of Shiny Cowbird trapping in management of the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*) in Puerto Rico. Blackbird nesting populations increased during effective cowbird control, complemented by a nest-box program. Cruz et al. recommended cowbird control as particularly effective for endangered species with small populations which lack effective responses to cowbird parasitism.

In Chapter 5, Chace et al. review the factors influencing the distribution and abundance of Brown-headed Cowbirds at different spatial scales. Although regions with higher overall cowbird abundance (for example, the north-central United States) tended to show higher cowbird parasitism, local and landscape level habitat factors are also important. Landscapes with the greatest forest cover and the fewest cowbird feeding areas had the lowest cowbird parasitism. Chace et al. observed the presence and distribution of residential areas and agricultural fields may also influence cowbird abundance and parasitism, as well as the better-known effects of feedlots or grazing animals. Their main message is the complex interrelationship among cowbird abundance and distribution, landscape structure, habitat types, and abundance and nesting success of different host species.

In Chapter 6, Goguen et al. discuss responses of female cowbirds to the presence of American bison (*Bison bison*) showing that females commuted longer distances to and from grazing bison. They also regularly foraged with elk (*Cervus elaphus*) or on a dry lake-bed without grazing. Goguen et al. suggested that larger cowbird home-range sizes might result in lower parasitism rates than in typical situations with grazing cattle.

In Chapter 7, Peer et al. summarize host defenses against parasitism by cowbird species. They noted that, while smaller species are hardest hit by cowbird parasitism and may fail to produce any young from parasitized nests, larger species may also have lower reproductive success due to competition with cowbird nestlings and costs of re-laying due to egg puncturing, removal, or depredation. They also note the costs and benefits to the hosts are associated with the main strategies of nest location and defense, nest desertion and egg burial, and egg ejection. Surprisingly, a number of potential or unsuitable host species will eject experimentally introduced cowbird eggs, even in the absence of actual parasitism by cowbirds. Peer et al. suggest that cowbird control programs may have a long-term cost, in that host defense would not be selected for and suggest scaling back cowbird control programs when host populations have increased substantially.

In Chapter 8, Rothstein and Peer continue in the same vein in their attempt to separate "fact" from "fiction" in cowbird control issues. They observe that, at least for Brown-headed Cowbirds, populations have declined in many areas in the last few decades and that cowbird parasitism is only one of several factors affecting host populations. They also argue that most bird species have been exposed to cowbird parasitism, even in the eastern United States, where cowbirds have been perceived as an invader. Given other problems, such as increased nest depredation and difficulties in maintaining suitable habitat, seen in fragmented habitats, Rothstein and Peer suggest that cowbird control efforts should be focused on those situations involving imperiled species known to be severely affected by cowbirds. This would allow scarce funding to be used for habitat preservation, restoration and other needs, rather than spending so much on cowbird control. They conclude with a series of basic questions that should be asked before cowbird control is begun, such as legal issues, development of explicit goals (with frequent evaluation of progress), and whether habitat or landscape-level management can accomplish the same goals as cowbird control.

Much still remains to be learned, particularly in less-studied regions such as the Caribbean Basin and other locations where host populations may be quite small, or about species such as Bronzed and Shiny cowbirds, which are still relatively little-studied. The symposium on which the volume was based occurred in 2003, and there has since been a wider recognition of the role of habitat-related issues in declines and recoveries of many bird species; however this volume still presents a valuable perspective on "the cowbird problem" and research needs. I recommend that anyone concerned with cowbird research or management consult this well-edited and interesting publication.—TIMOTHY BRUSH, Department of Biology, University of Texas-Pan American, 1201 West University Drive, Edinburg, TX 78539, USA; e-mail: tbrush@utpa.edu

HANDBOOK OF THE BIRDS OF THE WORLD. VOLUME 10. CUCKOO-SHRIKES TO THRUSHES. Edited by Joseph del Hoyo, Andrew Elliot, and David Christie. Lynx Edicions, Barcelona, Spain. 2005: 895 pp., 81 color plates, numerous color photographs and range maps. ISBN: 84-87334-72-5. $278.00

(cloth).—The Foreword for this volume is a review entitled *The Ecology and Impact of Non-indigenous birds* that is 19 pages in length and has a bibliography of 128 references. The bulk of this large format volume (31 × 34 cm; 4.2 kg) consists of 14 family accounts and 340 species accounts. The families covered are the Campephagidae (cuckoo-shrikes), Pycnonotidae (bulbuls), Chloropseidae (leafbirds), Irenidae (fairy-bluebirds), Aegithinidae (ioras), Ptilogonatidae (silky-flycatchers), Bombycillidae (waxwings), Hypocoliidae (Hypocolius), Dulidae (Palmchat), Cinclidae (dippers), Troglodytidae (wrens), Mimidae (mockingbirds and thrashers), Prunellidae (accentors), and Turdidae (thrushes). The family accounts vary in length from about five pages for each of the monotypic families (Hypocolius [*Hypocolius ampelinus*] and Palmchat [*Dulus domincus*]) to more than 100 pages for the thrushes. The family accounts are accompanied by color photographs, some full page, with, for example, 127 in the account for thrushes.

The family accounts begin with a range map and a summary of the habitat, number of taxa, and conservation status of the family. Then follow sections on Systematics, Morphological Aspects, Habitat, General Habits, Voice, Food and Feeding, Breeding, Movements, Relationships with Man, and Status and Conservation. There are no in-text citations, but a General Bibliography section contains author and year citations with the corresponding full citations in the References section at the end of the book. The species accounts begin with the French, German, and Spanish names, a list of other common English names, and then sections on Taxonomy, Subspecies and Distribution, Descriptive Notes (that includes descriptions of voice), Habitat, Food and Feeding, Movements, and Status and Conservation. There are no in-text citations, but the accounts end with a Bibliography. Each species account includes an easy-to-read range map in up to three colors. For the bird species I know best (e.g., Black-faced Cuckoo-shrike, *Coracina novaehollandiae*) I found the accounts accurate and the bibliography, although not exhaustive, included the major references. The References section is divided in two parts: References of Scientific Descriptions, and General List of References. The references number in the thousands. The Index is excellent, with common names double entered (e.g., Black-faced Cuckoo-shrike and Cuckoo-shrike, Black-faced).

The 81 color plates depict adult male and female plumage for dimorphic species and subspecies where there are distinct plumage differences. Juvenile plumages are described in the text. The plates are of universally excellent quality.

I find little to fault in this book or in the series. The family accounts are extensive and detailed, the species accounts succinct but informative, and the color plates excellent. The editors are to be congratulated on producing such a high-quality series. The price may be a bit much for some, but most libraries should have a copy.—WILLIAM E. DAVIS JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, MA 02536, USA; e-mail: wedavis@bu.edu

ALBATROSSES, PETRELS AND SHEARWATERS OF THE WORLD. By Derek Onley and Paul Scofield. Princeton Field Guides, Princeton University Press, Princeton, New Jersey. 2007: 236 pp., 46 color plates, and 136 maps. ISBN 0-691-13132-5. $29.95 (paper).—This slim volume is certain to replace weightier tomes in the gear of every seabirder. At just over 454 g (1 pound) and 150 by 225 mm (5½ by 8½ inches), it packs a lot of information in a small space. Smaller is not always better, but in the case of this guide the focus is on field identification, leaving details of their natural history to other sources, which is an excellent compromise.

This book covers 137 species in the Order Procellariformes. Preliminary sections cover issues in taxonomy as related to seabirds, family overviews, identification (and documentation), conservation, topography, and guidance on using the book. The plates have minimal but critical facing text, with common and scientific names, data on wing span and total length, the page where the text entry can be found, a brief overview of identification, information on the plumage illustrated (underparts, upperparts, age, gender, molt or plumage state, or subspecies), and cross-references to similar species. More information is conveyed within the text account including common and scientific names as well as alternate names, taxonomy, distribution, behavior relevant to field identification (flight behavior, boat-following, attraction to chum), and jizz.

The introductory material is useful to read, although most of us just dive into the plates when handed a field guide. The taxonomy of the book follows M. Brooke (2004, Albatrosses and petrels across the world, Oxford University Press, UK) with revisions from J. J. Austin et al. (2004, Auk 121:847–864) for small black-and-white shearwaters. The book would have benefited from a careful comparison of the text in the introduction with the text in the main body of the book. In the family section on storm-petrels, the group is split into two Subfamilies, Oceanitinae and Hydrobatinae, but in the text these are referred to as Southern Hemisphere and Northern Hemisphere groups. Another example is the observation that separating Westland Petrel (*Procellaria westandica*) from Parkinson's (*P. parkinsoni*) and White-chinned (*P. aequinoctialis*) petrels is "quick and easy" if the birds are in molt. This made me check the molt sections for these species, where I was informed that molt was after breeding. A check of the breeding section gave me the information, but it would have been much easier to include more information on molt timing in all species including the months they are in flight feather and body molt for breeding adults as well as non-breeders.

The plates seem to be technically well done but perhaps poorly reproduced. The mostly white heads of the albatross on the first three plates or other pale species are hard to discern from the white background. The jizz in the plates is generally quite good. I found myself wishing for a plate or line drawing showing a few species in markedly different winds as is common in hawk watching guides today. Some species are illustrated in molt showing contrasting old worn and new fresh feathers, and I found myself wishing for more of these useful illustrations of molting birds.

Tubenoses are poorly understood in terms of distribution and movements. We have little to no data for vast areas of the ocean and little information on seasonal changes. The mapped ranges are generally accurate for core ranges, with rarities or vagrants described in the text. Oddly, Band-rumped (Maderian) Storm-Petrel (*Oceanodroma castro*) is not shown to occur in the Gulf Stream off North Carolina, where it is regular, and it is not even described as a vagrant in this region. The text discusses storm-wrecked Band-rumpeds in Europe but not North America.

Regardless, this is a useful field guide that is well illustrated and easy to use. Typographical errors seem to be at a minimum. This guide is recommended to birders and ornithologists with an interest in seabirds. It will quickly replace Harrison's *Seabirds* as "the" additional bird guide on pelagic trips. I can't wait to use it in the field!.—MARY GUSTAFSON, Rio Grande Joint Venture Coordinator, Texas Parks and Wildlife Department, Mission, TX 78572, USA; e-mail: Mary.Gustafson@tpwd.state.tx.us

CURASSOWS AND RELATED BIRDS. By Jean Delacour and Dean Amadon. Updated by Josep del Hoyo and Anna Motis, paintings by Albert Earl Gilbert [et al.]. Lynx Edicions, Barcelona, Spain, in association with the American Museum of Natural History, New York, USA. 2004: 476 pp., 37 figs., 15 maps, and 56 color plates. ISBN: 84-87334-64-4. $75.00 U.S. (hardback).—Ever since I was aware of the existence of cracids, and saw my first Plain Chachalacas (*Ortalis vetula*) in the Santa Ana National Wildlife Refuge in south Texas in 1959, I have been enamored with them. I have gone on to specialize in the study of neotropical birds, mainly in Peru, and have had many delightful experiences with these wonderful birds. The highlight of all of my avian experiences was being with my good friend Gustavo del Solar R., then of Chiclayo in northern Peru, in September 1977 with the two of us making the first sightings of the White-winged Guan (*Penelope albipennis*) in exactly 100 years. I was delighted with the publication of the first edition of this book, which brought together what was then known of cracids and to be able to contribute some information to that volume. It was, however, the extraordinary paintings of Al Gilbert that made me spend many hours just poring over the book time after time. Gilbert made these birds come alive on the pages of the book and, especially, gave life like never before to the downy young, most of which had never been depicted.

When I heard that Al Gilbert, as well as Dean Amadon, was intent on seeing the book updated I was delighted. Although Jean Delacour was no longer alive, Gilbert hoped to see a second edition published before the death of Amadon. After much work and many false starts, some funding for additional artwork was found and Josep del Hoyo of Lynx Editions agreed the project should be published and that Lynx would take on the task. Instead of incorporating the new material into the existing book, the decision was made to add an updated section that would stand alone and be placed at the end of the original text.

The book is presented in two parts, the first of which is the original book with the addition of a Foreword to the new edition, written by Dean Amadon before his death, an Artist's Preface to the new edition, written by Al Gilbert, and Notes about the present edition. The color plates have been grouped between the original book and the updated section, with four black-and white figures having been eliminated and the color plate of the White-winged Guan replaced by a new one that Al Gilbert asked me to paint for the new edition. The new edition also contains a number of new plates of both adults and chicks, and in addition the five color plates from the "*Handbook of the Birds of the World*" are included. Additionally, there are four field studies painted by George M. Sutton in northern Mexico and a portrait of the Red-faced Guan (*Penelope dabbenei*) painted in Bolivia by Daniel F. Lane.

The book itself is a classic, but it is the amazing amount of new material that has been amassed for most species since the original volume was published in 1973 that is impressive. The second section of the new edition is devoted to a species by species accounting of this new information. A number of taxonomic changes cover forms considered as subspecies in the first book that are now recognized as full species, and their updated account is presented in the context of their present treatment. Each is also referenced, as are all updated accounts, to the original text. An example from the first book is the single species *Ortalis motmot*, with eight subspecies (*motmot*, *ruficeps*, *superciliaris*, *guttata*, *araucuan*, *squamata*, *subaffinis*, and *columbiana*) is regarded in the updates as three species, *Ortalis guttata* (with subspecies *auracuan*, *squamata*, *columbiana*, *guttata*, and *subaffinis*), *O. motmot* (with subspecies *motmot* and *ruficeps*), and the monotypic *O. superciliaris*. By cross-referencing these changes, and explaining their history, taxonomic changes are relatively easy to follow.

Some species, such as the White-winged Guan and the Horned Guan (*Oreophasis derbianus*) have gone from essentially unknown to very well known and from no birds in captivity to viable captive populations. The White-winged Guan was last seen in 1877 in mangroves in northern Peru, and had not been rediscovered when the first edition of the book was published in 1973; it was in fact, considered probably extinct! The old account covered less than one and one half pages, but the updated account in the new section of the book covers almost four pages and includes the history of its rediscovery, taxonomy, detailed natural history data, and a description of the captive breeding project that has now resulted in a number of wild hatched and reared birds from captive-bred parents. The Director of the project, Fernando Angulo P. (pers. comm.) has advised me the program has been sufficiently successful to no longer be necessary; the main focus will be on continuing the educational programs and the message about not hunting these magnificent birds. The Horned Guan was never considered to be extinct, but it was very poorly known and considered extremely rare. It is still not a common bird, but it has been found at additional sites since the writing of the original account, and the long-term studies of Fernando Gonzales-Garcia in Mexico have resulted in an amazing amount of data on its natural history. It too is represented by a healthy captive population but, to date, I do not believe that any individuals have been returned to the wild.

There are other species for which the status has changed drastically between the writing of the two parts of the book, and there are some, such as the Trinidad Piping Guan (*Pipile pipile*) that may be more well-known, but the population of which holds on by a thread. At present there are no Trinidad Piping Guans in captivity, but some educational programs are being conducted, especially focused on the cessation of hunting of this national treasure. I enjoyed reading the original text and then going to the new text, and comparing what has happened in the intervening 31 years. In most cases there is a great deal of additional information. Many younger biologists in the countries where these birds occur are devoting a great deal of time to learn as much as possible about them. Many of these people are habituating pairs of birds and following them as they go about their daily lives. Some have even been sufficiently lucky to be able to follow birds through courtship, nesting, and raising of the young. This persistence and dedication to these magnificent symbols of a healthy ecosystem is heartwarming. The authors of the original book, as well as those that compiled the updated accounts, are commended for putting together an incredible volume. I hope we will be able to have such a positive outlook if the book is updated in another 30 years! The details of the accounts are variable because they reflect the varying amount of information that is available.

Although this book has been reviewed several times, no one has said much about the illustrations. As an artist, I was overwhelmed by Al Gilbert's paintings in the first book, and his additions to the updated version are even better. His birds are extremely accurate, but better than that, they are ALIVE! His attention to the details of plants is also incredible. He acknowledges his debt to George M. Sutton, and I also must acknowledge Sutton's influence. Sutton once looked at one of my early paintings and asked me why I had spent so much time painting a beautiful bird but, at the same time, neglected the plants. I don't know if he ever asked that of Gilbert, but Gilbert did get the message that everything is important—and his plants are as stunning as his birds. Also following in Sutton's footsteps, Gilbert spent a great deal of time in the field making sketches of wild birds and plants, and he also spent a great deal of time at many aviaries to make sketches from living birds. In some cases Gilbert had to rely on photographs, but he is one of those artists who interprets photographs rather than copying them. He knows what you can and cannot take from a photo, or what must be changed. This is evident in his paintings (especially those of chicks, many of which had to be done from photos). Gilbert is a master at creating plates with multiple birds, but it is his stunning full-page portraits that leave one dumbfounded. Some that stand out for me are the Crested Guan (*Penelope purpurascens*) which, even without any background, is done as if one was looking at the bird with binoculars; I keep waiting for the bird to make the characteristic cracid headshake! I also can't take my eyes away from the Wattled Guan (*Abuuria aburri*) with its half-grown young perched on a cloud forest vine with bromeliads and tree ferns, and even a spider web, all with the ever-present raindrops waiting to drip to the next level. Then there is a pair of Highland Guans (*Penelopina nigra*) in their cloud forest home—but they are basically in the shadows with only spots of sunlight dappling their bodies and the surrounding vegetation. The pair of Nocturnal Curassows (*Nothocrax urumutum*) on the sunlight-spotted forest floor makes us believe that we now know something about this mysterious curassow that was not long ago thought to actually be nocturnal (rather than being a bird that sang mostly at night, but foraged like most curassows on the forest floor). There is also a portrait of a male to show the colorful facial skin and an eye that is simply alive! There are other paintings of adult birds that are equally stunning, like the Alagoas Curassow (*Mitu mitu*) and the field study portrait of a female Black Curassow (*Crax alector*), but the portraits and plates of downy young are equally good—or in some cases even better! The downy Northern Helmeted Curassow (*Pauxi pauxi*) makes one believe that the head of a parent will offer it a tidbit as it hops down from the root it is standing on. The downy Blue-billed Curassow (*Crax alberti*) gives us hope for the future of this very restricted range species.

Both the White-winged Guan and the Horned Guan are represented by plates showing the development from downy chick to adult. Of special interest for the latter is how the "horn" develops; the series of White-winged Guan paintings show the development of the white primaries as well as that of the unique two-toned beak. Additionally there are a number of composite plates of chicks, all equally well done. I am not sure who learned that many young curassows show sexual dimorphism in cere and eye color from hatching, but I suspect it was Al Gilbert. Only the artist looks at his subject so much and in so much detail as to discover these subtle characters! These characters are illustrated in several of the composite plates of chicks.

There are few groups of birds that so characterize the Neotropics and we are fortunate not only that Delacour and Amadon wrote the first book, but that Al Gilbert worked tirelessly and was able to convince Josep del Hoyo and Anna Motis to write and publish the updated edition. It is obvious that Gilbert considers cracids to be among his favorite birds—and his paintings and plates in this volume show this incredible love for these birds. The book is more than a reference volume—scientists, birders who want to learn about cracids, and even artists will want to own it. I would consider it to be one of the best bird family books of recent times. With 56 color plates its $75.00 (U.S.) price is not out of line.—JOHN P. O'NEILL, 3893 FM 1774 Road, Anderson, TX 77830, USA; e-mail: Pardusco@aol.com

The Wilson Journal of Ornithology 119(4):784–798, 2007

PROCEEDINGS OF THE EIGHTY-EIGHTH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The eighty-eighth annual meeting of the Wilson Ornithological Society (WOS) was held Thursday, 22 March, through Sunday, 25 March 2007 at the Sheraton Colonial Hotel, Wakefield, Massachusetts, at the invitation of the Massachusetts Audubon Society (Mass Audubon), and sponsored by the Houghton Mifflin Company and the Nuttall Ornithological Club. Wayne Peterson, Director of Mass Audubon's Important Bird Areas Program, chaired the Local Committee, which also included Taber Allison, Shawn Carey, Sandy Cofran, William Davis, Scott Edwards, Ellen Garcia, John Kricher, Carolyn Marsh, Betty Petersen, Robert Stymeist, Jeremiah Trimble, and Susie Vancura. On Saturday, 24 March, the WOS met jointly with Mass Audubon's Annual Birder's Meeting.

The WOS Council met from 1300 to 1800 hrs on Thursday, 22 March, in the Franklin Room of the Sheraton Colonial Hotel. That evening there was an "ice-breaker" reception for the conferees and guests.

The opening session on Friday convened in the Grand Ballroom at 0800 hrs with welcoming remarks from Wayne Peterson and WOS President Doris J. Watt. WOS First Vice President E. Dale Kennedy offered comments on the scientific program. The opening ceremony concluded with a presentation by Edward H. Burtt Jr., "Alexander Wilson: peddler, poet, pedagogue, and father of American ornithology."

The scientific program included 45 contributed papers and 25 contributed posters, which were organized into four paper sessions, a poster session, and a symposium on radar studies of avian migration. In addition, WOS hosted the Margaret Morse Nice Lecture, described below, and Mass Audubon hosted four feature presentations, "Arctic wings: birds of the Arctic National Wildlife Refuge" by Stephen Brown, "Marshes: the disappearing Edens" by William Burt, "Conservation of birds in open habitats in New England" by Robert Askins, and "Shorebirds by impression: a simpler method of field identification" by Kevin Karlson.

The evening program on Friday included a reception at the Harvard Natural History Museum hosted by the Nuttall Ornithological Club. The reception was followed by the Margaret Morse Nice Lecture, "Not exactly your 'nice' sparrow," by Douglas W. Mock and Patricia L. Schwagmeyer.

In addition to informal birding forays in the vicinity of the Sheraton Colonial Hotel on Friday and Saturday mornings, two longer trips were scheduled for Sunday: one to Parker River National Wildlife Refuge (Plum Island), and the other to Cape Ann. Both venues are premier birding sites in the state.

The attendees enjoyed a 60-min social gathering prior to the annual banquet, which was held in the Grand Ballroom of the Sheraton Colonial Hotel. After an enjoyable dinner, WOS President Doris J. Watt introduced Wayne Peterson, Chair of the Local Committee, who joined those assembled in thanking the many people whose hard work had resulted in a successful conference. President Watt also thanked the three elected members of council who had completed their terms of office, Mary Bomberger Brown, Robert Curry, and James Hill and welcomed the three newly elected members of council, Rebecca Holberton, Robert S. Mulvihill, and Timothy J. O'Connell. The following WOS awards and commendations also were presented:

MARGARET MORSE NICE MEDAL

(for the WOS plenary lecture)

Douglas W. Mock and Patricia L. Schwagmeyer, "Not exactly your 'nice' sparrow."

EDWARD'S PRIZE

(for the best major article in volume 118 of *The Wilson Journal of Ornithology*)

Cynthia A. Staicer, Victoria Ingalls, and Thomas W. Sherry, "Singing behavior varies with breeding status of American Redstarts (*Setophaga ruticilla*)."

WILLIAM AND NANCY KLAMM SERVICE AWARD

(for distinguished service to the Wilson Ornithological Society)

George A. Hall is the first recipient of this new award.

LOUIS AGASSIZ FUERTES AWARD

Corey Tarwater, "Natal dispersal and juvenile survival in a neotropical passerine."

PAUL A. STEWART AWARDS

Lauren MacDade, "Aquatic contribution to diet and consequences for refueling performance in spring migrant landbirds."

Kristen M. Covino, "The role of energetic condition in the motivation and orientation of migrant songbirds in the Gulf of Maine."

Jennifer Mortensen, "Conservation ecology and social organization of the endangered White-breasted Thrasher on St. Lucia, West Indies."

Michael J. Kuehn, "Determinants of male parental care in a socially monogamous avian mating system with promiscuity."

ALEXANDER WILSON PRIZE

(for best student paper)

Kara Belinsky, "Are color and song redundant signals of male quality in Chestnut-sided Warblers?"

LYNDS JONES PRIZE

(for best student poster presentation)

Jason Hill, "Preliminary analysis of post-fledging movements of female and fledgling Saltmarsh Sharp-tailed Sparrows."

NANCY KLAMM BEST UNDERGRADUATE STUDENT ORAL PAPER AWARD

Kelly Hallinger, "Does mercury contamination affect bird song?"

NANCY KLAMM BEST UNDERGRADUATE STUDENT POSTER AWARD

Megan Fitzpatrick, "Nest structure, incubation, egg viability and sex ratios in Tree Swallows in Michigan."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Ashley Peele, Ohio Wesleyan University, "Comparison of occurrence and abundance of feather-degrading *Bacilli* in different populations of Swamp Sparrows."

Lauren Smith, Ohio Wesleyan University, "Colorful parrot feathers inhibit bacterial degradation."

Jen Mortensen, Villanova University, "Conservation ecology and social organization of the endangered White-breasted Thrasher on St. Lucia, West Indies."

Kristen Covino, University of Maine, "The role of energetic condition in the motivation and orientation of migrant songbirds in the Gulf of Maine."

Susan Smith, University of Rhode Island, "Importance of fruit resources for migratory passerines during autumn stopover in southern New England."

Selection committee for the Nice Medal—Charles R. Blem, Doris J. Watt, William E. Davis Jr.; for the Edwards Prize—James A. Sedgwick; for the Klamm Service Award—Sara R. Morris (Chair), William E. Davis Jr., Jerome A. Jackson, Doris J. Watt; for the Fuertes and Stewart Awards—Robert B. Payne (Chair), Laura Payne, David W. Steadman; for the Alexander Wilson Prize, the Lynds Jones Prize, and the Nancy Klamm undergraduate presentation awards—Jameson F. Chace (Chair), William Brown, Chris S. Elphick, Chris Farley, Pamela Hunt, Danny J. Ingold, James D. Rising, Margaret A. Voss, Jeffrey R. Walters, Douglas W. White; and for the WOS Travel Awards—Timothy J. O'Connell (Chair), Mary Bomberger Brown, Mia Revels.

COMMENDATION

WHEREAS Sara R. Morris served the Wilson Ornithological Society for 6 years in the role of Secretary, and

RECOGNIZING her encyclopedic knowledge and understanding of the procedures and traditions regarding how the Society conducts its business, and

RECOGNIZING that four presidents depended upon her unmatched organizational skills and attention to detail, and

RECOGNIZING that as secretary, many people have first contacted the Society through her, and that her welcoming nature has made her one of the most effective ambassadors of the Society,

THRERFORE BE IT RESOLVED that the Wilson Ornithology Society fondly extends its appreciation for her service and friendship.

COMMENDATION

WHEREAS James A. Sedgwick began serving as the Editor of *The Wilson Bulletin* in 2004, and

RECOGNIZING that he continued and accelerated the transition from paper to electronic communication, thus increasing the efficiency of the editorial process, and

RECOGNIZING that he was successful in publishing the journal on time, and

RECOGNIZING that through his initiative the journal underwent a significant redesign, including exciting new cover art and a change of name to *The Wilson Journal of Ornithology*,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society thanks James A. Sedgwick for his valuable service in producing the Society's premier publication.

COMMENDATION

WHEREAS Kathleen Beal served an extraordinary 20-year term as the Index Editor of *The Wilson Bulletin* and its successor, *The Wilson Journal of Ornithology*, and

RECOGNIZING that as her expertise in multivariate statistical applications frequently exceeded those of referee and editor alike, her service on the Editorial Board was invaluable,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society extends its sincere gratitude to Kathleen Beal for her outstanding service to this Society.

COMMENDATION

WHEREAS Doris J. Watt has for the past 2 years served the Wilson Ornithological Society in the role of President, and

RECOGNIZING that this tenure is a continuation of many years of service to the Society, including a decade-long commitment in the important role of Treasurer, and

RECOGNIZING that as President, her accomplishments include revitalizing the committee structure of the Society, establishing new committees, resurrecting inactive committees, and defining the roles and duties of the various committees, and

RECOGNIZING that as President, she has maintained a clear vision of the identity of the Society, participating fully in the North American Ornithological Conference, but also returning to our roots in smaller venues,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society offers its sincere gratitude to Doris J. Watt, and looks forward to her contributions in her new role as Past President.

All of the commendations were enthusiastically passed by acclamation.

Soon-to-be WOS Past President Doris J. Watt concluded the awards ceremony with what may become a new WOS tradition: she handed a ceremonial gavel to incoming WOS President James D. Rising.

BUSINESS MEETING

President Doris J. Watt called the annual business meeting to order at 1615 hrs, Friday, 23 March 2007 in the Grand Ballroom of the Sheraton Colonial Hotel, and noted that a quorum was present. Secretary John A. Smallwood presented a synopsis of the previous day's Council meeting, noting that as of 1 March 2007, the Society's membership stood at 1753 individuals, including 214 students and 69 new members of all membership categories. While the renewal cycle was still underway, at that time the retention rate was 87%. In addition, 464 libraries and institutions subscribed to *The Wilson Journal of Ornithology*, which represented an increase over the 417 subscriptions the previous year. The secretary then asked those assembled to stand in recognition of the following members who had died since we last met: William A. Burnham (Boise, ID), William H. Elder (Columbia, MO), Phyllis L. Hurlock (Honey Brook, PA), Laurence R. Jahn (Custer, WY), Horace H. Jeter (Shreveport, LA), Harold F. Mayfield (Toledo, OH), Katherine G. McNaughton (St. Petersburg, FL), Elsie Richey (Hayward, CA), and Jan Roger Van Oosten (Seattle, WA).

Secretary John A. Smallwood informed those present that Council had approved of continuing our practice of offering free 1-year memberships to nonmember students who make presentations at the annual meetings, and was pleased to announce that 40 students were receiving free memberships this year. Council was grateful to the Investing Trustees for their astute care of the society's investments, which they manage for total return, i.e., both income and capital appreciation. Council also expressed gratitude to Robert L. Curry and the new Web Site Committee, and Secretary Smallwood encouraged those assembled to "check it out." Finally, Secretary Smallwood announced that Council had unanimously re-elected Clait E. Braun as Editor of *The Wilson Journal of Ornithology* for 2008 and reiterated Council's deep appreciation to Editor Braun for the very high standard that this journal represents.

Allan Keith, Chair of the Finance, Audit, and Investment Committee, presented the Treasurer's report for Treasurer Melinda Clark in her absence. Editor Clait E. Braun presented the editor's report for himself.

Sara R. Morris, Chair, presented the report of the Nominating Committee, which also included Mary Bomberger Brown, Edward H. Burtt Jr., and Douglas W. White: President, James D. Rising; First Vice-President, E. Dale Kennedy; Second Vice-President, Robert C. Beason; Members of Council 2007–2010 (3 nominees for 3 positions), Robert S. Mulvihill, Rebecca Holberton, and Timothy J. O'Connell; and a 1-year replacement (2007–2008) for Council Member Kathy Beal, who resigned in February, Robert L. Curry. Having asked for additional nominations from the floor and hearing none, President Doris J. Watt closed the nominations as a result of a motion by Peter Stettenheim, seconded by Daniel Klem Jr. that was unanimously passed by voice vote. Further, Sara R. Morris moved and Jerome A. Jackson seconded that the secretary cast a single unanimous vote for the slate of nominees, and by acclamation, it became so.

Frank Moore, host of the 2008 annual meeting, delivered an informative presentation on the new venue; the meeting will take place in Mobile, Alabama, 17–20 April 2008. Todd Katzner and Robert Mulvihill will host the 2009 meeting in Pittsburgh; early plans are to meet in April, but the exact dates are to be determined. WOS participation in a North American Ornithological Conference in 2011 is still in the early planning stages.

Having completed the business at hand, President Watt inquired if any of those assembled had additional items of business. None did. Instead, Timothy J. O'Connell moved and Sara Morris seconded that we adjourn. This happened at 1640 hrs.

REPORT OF THE TREASURER

Statement of Revenues and Expenses For the Year Ending 31 December 2006.

	2006 12 Months Actual	2006 Annual Budget	2007 Annual Budget	2008 Annual Budget
Revenues				
Contributions	$ 1,189	$ 1,000	$ 1,200	$ 1,200
Student Travel Research Fund	624	—	—	—
Van Tyne Library Book Fund	140			
Sales - back issues	444	—	518	518
Sales - books - Van Tyne Libr.	—	900	500	500
Subscriptions	17,092	18,000	17,317	17,317
Page charges	19,966	16,750	15,506	15,506
Royalties	3,653	1,600	3,409	3,409
BioOne Electronic Licensing	10,760	10,055	10,760	10,760
Mailing list rental income	572	500	660	660
Memberships	34,149	40,000	31,332	31,332
Other income	10,000	2,000	—	—
Total revenues from operations	**$ 98,589**	**$ 90,805**	**$ 81,202**	**$ 81,202**
Expenses				
Journal publication costs:				
Editorial honorarium	$ —	$ —	$ 4,000	$ 4,000
Editor travel/supplies	3,537	230	1,000	1,000
Editorial assistance	55,349	55,000	25,000	25,000
Copyright expense	38	50	48	48
Printing - Journal	44,737	65,000	64,400	64,400
Artwork	300	—	—	—
Printing color plates	$ 580	$ 2,500	$ 2,400	$ 2,400
	$ 104,541	$ 122,780	$ 96,848	$ 96,848

Operating expenses:				
Postage & mailing - back issues	$ 978	$ 320	$ 440	$ 440
Storage - back issues	473	1,400	680	680
Van Tyne Library - expenses	629	1,500	1,500	1,500
OSNA management services	19,629	21,000	21,000	21,000
Credit card fees	1,506	1,200	1,100	1,100
Travel expenses-OSNA rep	—	1,800	1,500	1,500
Travel expenses - general	686	5,000	450	450
Travel expenses-Ornith Council	116	900	200	200
Meeting expenses	12,326	1,500	1,000	1,000
Membership expenses	—	—	—	2,000
Accounting fees	4,558	4,500	4,500	4,500
Insurance - D & O	1,425	1,500	1,425	1,425
Office supplies	531	300	570	570
Postage - general	47	260	260	260
Other expenses	141	250	—	35
Filing fees	5	5	5	5
Discretionary expenses	1,718	3,500	3,000	3,000
	$ 44,768	$ 44,935	$ 37,630	$ 39,665
Awards:				
Membership awards	$ —	$ —	$ —	$ 600
Hall/Mayfield	1,000	1,000	1,000	1,000
Stewart	3,000	3,000	3,000	3,000
Fuertes	2,500	2,500	2,500	2,500
Wilson, Lynds Jones, Klamm	—	1,200	1,200	1,200
Student travel grants	10,000	10,000	5,000	5,000
Nice award expenses	2,224	6,800	3,000	3,000
	$ 18,724	$ 24,500	$ 15,700	$ 16,300
Contributions:				
Support - Ornith Council	$ 9,000	$ 9,000	$ 9,000	$ 9,000
Support - Ornith Council, restricted to revision costs	—	—	7,500	—
Am Bird Conservancy Dues	—	250	250	250
AAZN dues	—	250	250	250
	$ 9,000	$ 9,500	$ 17,000	$ 9,500
Total Expenses	**$ 177,033**	**$ 201,715**	**$ 167,178**	**$ 162,313**
Expenses in excess of revenues before investment income	**$ (78,444)**	**$ (110,910)**	**$ (85,976)**	**$ (81,111)**
Investment activity:				
Revenues				
Investment earnings - budgeted	$ —	$ 70,000	$ —	$ —
Realized gain/loss - ML	67,407		23,612	23,612
Realized gains/losses-Howland	5,385		18,968	18,968
Realized gains/losses - Sutton	5,812		5,812	5,812
Unrealized gain/loss - ML	43,658		36,722	36,722
Unrealized gain/loss - Howland	191,624		29,887	29,887
Unrealized gain/loss - Sutton	15,368		4,794	4,794
Investment earnings - ML	30,071		20,000	20,000
Investment earnings - Howland	54,875		25,000	25,000
Investment earnings - Sutton	4,650		4,200	4,200
Total revenues from investment activity	**$ 418,850**	**$ 70,000**	**$ 168,995**	**$ 168,995**
Investment fees	**$ 26,114**	**$ 22,000**	**$ 25,091**	**$ 25,091**
Investment revenues in excess of expenses	**$ 392,736**	**$ 48,000**	**$ 143,904**	**$ 143,904**
Total revenues in excess of expenses	**$ 314,292**	**$ (62,910)**	**$ 57,928**	**$ 62,793**

STATEMENT OF FINANCIAL POSITION

31 December 2006

Assets		
Cash investments:		
Merrill Lynch—cash	$ 69,865	
Coamerica - Van Tyne checking	615	
Van Tyne Univ Michigan account	461	
Sutton Fund - cash equivalents	10,663	
Howland Mgmt - cash equivalent	69,940	
Total cash and cash equivalents		$ 151,544
Other Investments:		
Merrill Lynch—common stocks	716,230	
Merrill Lynch—corp bonds	49,990	
Merrill Lynch—mutual funds	28,268	
Sutton Fund—equities	141,786	
Sutton Fund—corp bonds	9,285	
Howland Mgmt—equities	1,378,768	
Howland Mgmt—fixed income	311,947	
Total Other Investments		2,636,274
Total Assets		$ 2,787,818
Fund Balances:		
Restricted funds—Sutton Fund	$ 161,735	
Unrestricted funds	551,135	
Net Income	314,294	
	865,429	
Fund balance–Klamm	1,760,654	
Total Fund Balances		$ 2,787,818

Melinda Clark, *Treasurer*

EDITOR'S REPORT

This report is for the period 1 July 2006–28 February 2007. The editorial offices of *The Wilson Journal of Ornithology* received 186 new manuscripts in 2006; 107 of those were received after 1 July 2006. We have rejected or requested withdrawal of 56 of the 186 manuscripts thus far with final decisions still pending for 16 while 44 are awaiting revisions. We do not expect all manuscripts awaiting revision to be returned or accepted. The remainder (70) have been or are scheduled to be published (some were in Volume 118) (9 are in the March 2007 issue of Volume 119, and 11 are in the June 2007 issue with 40 awaiting issue make up). The March 2007 issue should be mailed during the first week in March and will contain 27 Features and Short Communications plus Once Upon a Time in American Ornithology, Book Reviews, and an editorial for a total of 150 pages. The June 2007 issue is ready to be sent to Allen Press (to be shipped on 2 March) and has 27 Features and Short Communications, Once Upon a Time in American Ornithology, and Book Reviews. We expect it to be ~150 pages in length.

We presently have 57 accepted manuscripts awaiting publication. This number will completely fill the September and December 2007 issues. Thus, we are building a backlog. We can tighten the acceptance rate and have been slowly doing so. However, we received a substantial number of accepted or encouraged manuscripts from the Fort Collins office, most of which have now been fully processed, but 29 are still awaiting revision. Some of these will not be returned.

We have received 39 new manuscripts through 28 February 2007 (rate of 0.66 manuscripts received per day) and can expect the total received in 2007 to be ~240. Provided we publish 108 manuscripts (27 per issue) each year, we will have to reject or have withdrawn 132 manuscripts (55%). The manuscripts most likely candidates for rejection or withdrawal are from countries other than North America as most of these need extensive work. Prompt processing of manuscripts is a blessing, as it encourages authors and word spreads that the *WJO* is a speedy journal in terms of making decisions. The downside is that authors will eventually become discouraged about the length of time to publication even though the acceptance or rejection date may be within 1–2 months of submission. The other major factor is the peer review system. We may wish to increase the rejection rate but we really depend upon the referees. At least half of the referees are too kind. Our most difficult issues are finding suitable referees willing to review, obtaining timely reviews, and lack of rigor of reviews.

We are extensively using electronic mail and all reviewers are contacted by e-mail (a few by phone). Less than 5% of reviewers request paper copy and about the same percentage return paper reviews. We still return marked paper manuscripts and referee comments to authors with instructions to return a revised paper copy and an electronic file. All subsequent correspondence and editing are done electronically. We make exceptions for non-North America authors and will process all correspondence with them electronically when possible. We use a mix of electronic and paper correspondence with Allen Press, but still receive and return paper copy of page proofs. We are trying to eliminate one step in the page proof process which may eventually be a cost savings.

I am pleased with where we are in the process and we have a workable routine. We have not made any progress on recruiting Associate Editors although I have identified several good candidates. The basic issue is that most employers believe that all journals are well funded and will not allow release time for their valued researchers or professors unless these people can continue to work full time at their regular jobs. The past 8 months have convinced me that editing a major journal is no longer a part-time 'job' as one could spend most of his time working on editorial matters. This could be partly resolved by hiring more staff. This is not my desire. However, I can see how the editor job can be full time. The days of 'volunteer' editors are about over.

I look forward to continuing to serve the Wilson Ornithological Society.

Clait E. Braun, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

The first item of business for the Membership Committee will be to solicit two volunteers from WOS to serve on the committee. Primary duties of the Membership Committee include maintenance and distribution of the WOS display board and devising effective means to increase member recruitment and retention. The committee should be able to execute its charges through e-mail and telephone exchanges.

The display case arrived at its new home in Stillwater, Oklahoma in late December. Due primarily to the recent name change for the Journal, several modifications to the material presented in the display will be necessary. There are 10 panels of information on plastic posters with Velcro® backing affixed to the four large structural panels of the display itself. Just to make the change from *The Wilson Bulletin* to *The Wilson Journal of Ornithology* would require replacing five of the plastic panels, and probably replacing a sixth to illustrate what the new Journal looks like. Other information on those five crucial panels should be fact-checked and amended as appropriate.

Several of the panels in the display contain scanned artwork and copies of Journal covers through the history of the WOS. Thus, updating the display is more complicated than simply retyping the text. The Chair is currently in the process of tracking down electronic files of all the information included in the display. Once located and updated, these files should be archived, most likely in the Josselyn Van Tyne Memorial Library.

Due to the difficulty in updating the display without the files, the display will not be updated in time for the 2007 meeting in Wakefield, MA. We do intend, however, to ship the display to Wakefield for the meeting, and encourage all WOS council and committee members to spend some time at the display to answer questions and help recruit new members. Many of the meeting attendees will not already be WOS members, so this joint meeting with Mass Audubon is a wonderful opportunity to recruit new members.

Once the display has been updated, the Membership Committee will, on advice of Council, revisit the schedule of its deployment. For example, given sufficient shipping funds and a local WOS member willing to ensure that the display gets set up, taken down, and shipped to the next location, we could potentially have the display set up at multiple venues annually. These include annual meetings of other professional societies, birding festivals, etc.

Timothy J. O'Connell, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

I am very pleased to submit this report of the activities at the Josselyn Van Tyne Memorial Library for the period 1 January to 31 December 2006. The following happened over the past calendar year with respect to the library.

Loans

Loans of library materials to members included 27 transactions to 16 members. These loans included books loaned, and 87 copied and scanned articles.

Acquisitions

Exchanges: A total of 142 publications in 110 exchanges was received by exchange from 110 organizations or individuals.

Gifts: We received 29 publications from 25 organizations.

Subscriptions: We also received 36 publications from 25 subscriptions. We spent a total of $695.68 on subscriptions in 2006.

Donations: Members and friends donated 321 items. These donations included 235 books, 84 journal issues, and 1 report.

Donors: The five members and friends donating materials include: Sherri Smith, E. O. Willis, Paul Ehrlich, The Peregrine Fund, and the American Federation of Aviculture.

Purchases: New items purchased for $190.35 included 1 book and 16 journal issues and volumes.

Dispersals

Gifts to Other Institutions: We sent 48 journal issues to two other institutions.

Back Issues: We sent out seven back issues of *The Wilson Bulletin* for only the cost of postage.

Duplicates: We sold 77 duplicate books and journal issues for $159.00.

Accessibility on the Web

Web Site: The web site (http://www.ummz.umich.edu/birds/wos/) continues to provide access to the library. Journals currently received are listed on the site as well as how to access the University of Michigan's on-line catalogue, which interested people can use to check holdings.

Books for Sale: We have our duplicate books for sale listed on the web site.

Journals for Trade: Also listed on the web site are the journals we have available for sale or trade.

Thank You's

Janet Hinshaw has done a wonderful job as the Wilson Ornithological Society Librarian. Many thanks to our secretary, Janet Bell, for keeping the library loan records and to our work-study students Rebecca Carter and Marie Sweetman for copying and scanning articles, keeping the library running, and mailing out back issues of *The Wilson Bulletin.*

Robert B. Payne, *Chair*

REPORT OF THE PUBLICATIONS COMMITTEE

During the course of last spring and summer Council transitioned the role of Editor of *The Wilson Journal of Ornithology* from James A. Sedgwick, whose employer was increasingly unwilling to support the editorial office, to Clait E. Braun, who was in a position to help support the office. Jim has served admirably as Editor and has been responsible for reformatting the recently renamed Journal, a process that should serve the Society admirably in the future. We thank him for his valuable service and, at the same time, welcome former Society President Clait E. Braun as the new Editor. Furthermore, we ask that Council unanimously re-elect Clait E. Braun

Editor for *The Wilson Journal of Ornithology* for Volume 120 (2008).

There is a large and growing resistance of employers to provide editorial support to any journals. Even Associate Editors now have to carve time from their regular activities without any relief from their employing agency. The attitude seems to be growing that professional societies that produce journals have sufficient funds to contract most actual editorial activities to professional groups. Council should be aware of this situation and may want to develop a plan regarding how the Society will handle Editor vacancies in the future. The days of "volunteer" editors are numbered. The best scenario may be to hire an Editor and to use a commercial group to produce the Journal. Doing so will cost more than at present, but it will cost less than hiring a commercial group.

On-line publishing is being tackled head on by some professional societies. So far on-line publishing appears to be having a negative effect on society membership retention rates and on attracting new members. This may cause some professional societies to merge. This is actually being considered by some groups. Back issues (as individual articles) of our Journal and its predecessor currently are available on-line either through BioOne, JSTOR, or SORA. The Committee recommends against publishing only on-line or of offering the option of paper or on-line receipt of the Journal.

Keith L. Bildstein, *Chair*

REPORT OF THE WEB SITE COMMITTEE

Summary of Committee Activities

Management of web site up to December 2006—Janet Hinshaw continued her long-standing service as manager of the WOS web site until mid-December 2006. The site is hosted by the University of Michigan, in conjunction with the Bird Division of the Museum of Zoology; the original home page was at http://www.ummz.lsa.umich.edu/birds/wos.html.

Creation of revised web site—In December 2006, I developed a new version of the web site, relying heavily on previously existing pages but incorporating the following changes:

- Addition of standardized navigation bar at the top of all pages, with pull-down menus for access to subsidiary pages within major sections. The sections at present are: About WOS, Membership, Publications, Meetings, Awards, and Library.
- Addition of pages for the 2007 Annual Meeting in Boston.
- Addition of pages for new WOS Awards (Klamm Award, Nancy Klamm undergraduate awards).
- Expansion of pages listing WOS Past Presidents and other historical pages.

The revised site has a new home page URL (http://www.ummz.umich.edu/birds/wos/index.html) that is structured to separate WOS pages more clearly from UM Bird Division web pages. All WOS pages are now in the single WOS directory, with additional subdirectories for most of the major sections listed above.

The site continues to be hosted by the University of Michigan. Management of the site presently passes through UM staff person John Megahan; Bob or Janet sends pages to John for addition to the site.

Expenses and Budget Request

Expenses for 2006 to 2007—None.

Budget request for 2007 to 2008—The committee requests funds for licensing a new domain name for the web site, hoping for www.wilsonsociety.org (www.wos.org is already in use, by the Washington Ornithological Society). Cost: $35 per year (Network Solutions).

Additional funds may be needed to compensate a new web site host. If we can arrange hosting using the new domain name through a university (e.g., Canisius College), there may not be any cost. If we go with a commercial web hosting company, the cost would be approximately $250 per year.

Items for Council Action

- Approval of 'purchase' of domain name (host name) for the WOS web site.
- Approval of the plan to move the web site to a new host that would permit direct ac-

cess (for uploads and edits) by the web manager = Web Site Committee Chair (Curry).

- Input to committee concerning information to be added to web site.

Robert L. Curry, *Chair*

REPORT OF THE SCIENTIFIC PROGRAM COMMITTEE

The Committee on the Scientific Program was chaired by WOS Second Vice-President E. Dale Kennedy, who was assisted by session moderators Chris Elphick, Brice Hanberry, Rebecca Holberton, Austin Hughes, David Lahti, Kathy Martin, Benjamin Taft, and Margaret Voss. The symposium on radar studies of migration was organized by Robert C. Beason.

PAPER SESSIONS

Radar Symposium

Michael Begier, USDA/APHIS Wildlife Services, Raleigh, NC, and Robert C. Beason, USDA/APHIS/WS National Wildlife Research Center, Sandusky, OH, "Nocturnal movements of waterbirds along the North Carolina coast."

Bill Evans, Old Bird, Inc., Ithaca, NY, "Comparison between acoustic and radar migration data."

Sidney A. Gauthreaux Jr., Mary Anna Hanna, and Carroll G. Belser, Radar Ornithology Laboratory, Department of Biological Sciences, Clemson University, Clemson, SC, "The seasonal temporal pattern of Purple Martin roosting behavior in relation to latitude."

Rhonda Millikin, EchoTrack, Inc., Ottawa, ON, "Avoidance of wind turbines by night migrating birds."

Dave Mizrahi, Robert Fogg, and Patti Hodgetts, Research and Monitoring Department, New Jersey Audubon Society, Cape May Court House, NJ, "Flight patterns of migrating birds in the Appalachian Mountains and mid-Atlantic coastal plain: a comparison using portable X-band radar."

General Sessions

Karen Aghababyan and Armen Asryan, Environmental Conservation Research Center, American University of Armenia, Yerevan, Armenia, Hayt Harutyunyan, Lusine Stepanyan, and Maro Kochinyan, Biological Department, Yerevan State University, Yerevan, Armenia, and Renee Richer, Weill Cornell Medical College in Qatar, Doha, Qatar, "Current condition of the White Stork (*Ciconia ciconia*) in Armenia."

Michael Allen, Jim Sheehan, and Terry Master, Department of Biology, East Stroudsburg University, East Stroudsburg, PA, "Comparing Acadian Flycatcher (*Empidonax virescens*) breeding biology in healthy versus adelgid infested hemlock stands."

Stephen Agius and Rebecca Holberton, Department of Biological Sciences, University of Maine, Orono, ME, "Changes in energetic condition as a function of parental expenditure in Arctic and Common terns."

Trina Bayard and Chris Elphick, Department of Ecology and Evolution, University of Connecticut, Storrs, CT, "Pausing to reflect: an examination of how we study avian area sensitivity."

Kara Loeb Belinsky, Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA, "Are color and song redundant signals of male quality in Chestnut-sided Warblers?"

Luke K. Butler, Department of Biology, Tufts University, Medford, MA, "Timing and location of prebasic molt in northern populations of Vermilion Flycatchers."

Jameson F. Chace, Department of Biology and Biomedical Sciences, Salve Regina University, Newport, RI, and Steven D. Faccio, Conservation Biology Department, Vermont Institute of Natural Science, Woodstock, VT, "Canada Warbler territory characteristics and pairing success in northeastern Vermont."

Paul J. Champlin, J. Drew Lanham, and Victor B. Shelbourne, Department of Forestry and Natural Resources, Clemson University, Clemson, SC, and John C. Kilgo, Southern Research Station, USDA Forest Service-Savannah River, New Ellington, SC, "Landscape ecosystem classification of Henslow's Sparrow habitat on the South Carolina upper coastal plain."

Adam E. Cirone and Danny J. Ingold, Biology Department, Muskingum College, New Concord, OH, "The impact of vegetation structure and composition on grassland bird species density on a reclaimed strip-mine in southeastern Ohio."

Anne Condon and Daniel A. Cristol, Department of Biology, College of William and Mary, Williamsburg, VA, "Mercury levels in newly independent Eastern Bluebirds (*Sialia sialis*) along the contaminated South River, VA."

Kristen M. Covino and Rebecca L. Holberton, Department of Biological Sciences, University of Maine, Orono, ME, "The role of energetic condition in the motivation and orientation of migrant songbirds in the Gulf of Maine."

David DesRochers and J. Michael Reed, Department of Biology, Tufts University, Medford, MA, "Hawaiian Moorhen calls, response to playback, and comparison of survey methods."

Carla J. Dove, Marcy Heacker, and Nancy Rotzel, Feather Identification Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C., "Using DNA barcodes to identify birds involved in bird/aircraft collisions."

Scott L. Friedman and Daniel A. Cristol, Department of Biology, College of William and Mary, Williamsburg, VA, "Elevated mercury levels in a terrestrial songbird."

Ana Gabela and Jeffrey Podos, Department of Biology and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA, "Diversity and abundance of terrestrial birds surrounding an urban center on Santa Cruz, Galápagos Islands."

Andy Glass and Bryan Watts, Center for Conservation Biology, College of William and Mary, Williamsburg, VA, "Osprey foraging efficiency and population dynamics."

David S. Goodyear V and E. Dale Kennedy, Biology Department, Albion College, Albion, MI, "Does the source of DNA matter? A comparison of DNA extracted from feathers and blood of nestling House Wrens and Tree Swallows."

Erin Hagen, College of Forest Resources, University of Washington, Seattle, WA, and Coral Wolf, School of Natural Resources, University of Michigan, Ann Arbor, MI, "Breeding ecology of the Juan Fernández Firecrown and the Green-backed Firecrown on Robinson Crusoe Island, Chile."

Kelly K. Hallinger, Katherine A. Kazmer, Daniel J. Zabransky, and Daniel A. Cristol, Department of Biology, College of William and Mary, Williamsburg, VA,"Does mercury contamination affect bird song?"

Brice Hanberry, Phillip Hanberry, Stephen Demarais, and Jeanne C. Jones, Department of Wildlife and Fisheries, Mississippi State University, Mississippi State, MS, "Avian assemblages of intensively established pine plantations in Mississippi."

Rebecca L. Holberton, Laboratory of Avian Biology, University of Maine, Orono, ME, and Peter P. Marra, Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C., "The role of food availability in driving physiological carry-over effects from the non-breeding to the breeding season."

Austin L. Hughes and Mary Ann K. Hughes, Department of Biological Sciences, University of South Carolina, Columbia, SC, "Coding sequence polymorphism in mitochondrial genomes reflects population histories."

Danny J. Ingold and James L. Dooley, Biology Department, Muskingum College, New Concord, OH, and Nicole Cavender, The Wilds, Cumberland, OH, "Nest-site fidelity in grassland birds: six years of data from The Wilds, a reclaimed stripmine."

Cara Joos and Martha Desmond, Department of Fisheries and Wildlife, New Mexico State University, Las Cruces, NM, and Rebecca Holberton, Department of Biological Sciences, University of Maine, Orono, ME, "Are shrub encroached grasslands sub-optimal habitat for wintering Sage Sparrows (*Amphispiza belli*)?"

David Lahti, Department of Biology, University of Massachusetts, Amherst, MA, "Experimental and comparative evidence that egg pigment protects embryos from the sun."

Thomas Litwin, Department of Biological Sciences, Smith College, Northampton, MA, Trevor Lloyd-Evans, Manomet Center for Conservation Sciences, Manomet, MA, and Katherine Halvorsen, Department of Mathematics and Sciences, Smith College, Northampton, MA, "Stopover habitat use by neotropical spring migrant land birds in the Connecticut River Valley."

Wayne Meyer, Biology Department, Austin College, Sherman, TX, "Do subadult Painted Buntings sing the same songs as adults?"

Scott McConnell and Timothy J. O'Connell, Department of Zoology, and David M. Leslie Jr., Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University, Stillwater, OK, "Breeding habitat and estimated population size of Mountain Plover in Oklahoma."

Jennifer Mortensen and Robert Curry, Department of Biology, Villanova University, Villanova, PA, "Conservation ecology and social organization of the endangered White-breasted Thrasher on St. Lucia, West Indies."

Ashley M. Peele and Edward H. Burtt Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH, and Russell Greenberg, Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C., "Comparison of occurrence and abundance of feather-degrading *Bacilli* in different populations of Swamp Sparrows."

Guadalupe Quiroz and Diane L. H. Neudorf, Sam Houston State University, Huntsville, TX, "Responses of Carolina Wren nestlings to parental alarm calls."

Steven E. Reinert, Block Island Banding Station, Barrington, RI, "Mist-net capture bias during fall migration on Block Island, Rhode Island."

Matthew D. Reudink, Sean P. Mullen, and Robert L. Curry, Department of Biology, Villanova University, Villanova PA, and Stephen G. Mech, Albright College, Reading, PA, "Structure and dynamics of the hybrid zone between Black-capped and Carolina chickadees in southeastern Pennsylvania."

James W. Rivers and Stephen I. Rothstein, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, "Exaggerated begging is not an adaptation for brood parasitism in the Brown-headed Cowbird."

Lauren A. Smith and Edward H. Burtt Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH, Jenna Sroka and Max R. Schroeder, Department of Botany-Microbiology, Ohio Wesleyan University, Delaware, OH, and Kevin McGraw, School of Life Sciences, Arizona State University, Tempe, AZ, "Colorful parrot feathers inhibit bacterial degradation."

Susan B. Smith and Scott R. McWilliams, Department of Natural Resources Science, University of Rhode Island, Kingston, RI, "Importance of fruit resources for migratory passerines during autumn stopover in southern New England."

Jack M. Stenger and Edward H. Burtt Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH, "Pattern of wear among tail feathers of songbirds."

Benjamin Taft, Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA, "Geographic and temporal variation in Tree Swallow (*Tachycineta bicolor*) song repertoires: evidence for song learning as adults."

Mark Vukovich and John C. Kilgo, Southern Research Station, USDA Forest Service-Savannah River, New Ellington, SC, "Effects of snag density on territory dynamics of Red-headed Woodpeckers."

POSTERS

Bill Brown, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE, "Avian community composition and abundance in forest remnants."

Peggy E. Buckley, Arthur R. Clark, H. David Sheets, and Sara R. Morris, Departments of Physics and Biology, Canisius College, Buffalo, NY, "An analysis of avian migration based on western New York television tower mortality and banding data."

Steven P. Campbell and Malcolm L. Hunter Jr., Department. of Wildlife Ecology, University of Maine, Orono, ME, and Jack W. Witham, Holt Research Forest, University of Maine, Arrowsic, ME, "Long-term changes in spatial distribution of birds responding to small-scale disturbances."

Christine M. Caron and Peter W. C. Paton, Department of Natural Resources Science, University of Rhode Island, Kingston, RI, "Harlequin Duck population trends and habitat use in Rhode Island."

V. S. Cavalieri, T. J. O'Connell, and D. M. Leslie Jr., Department of Natural Resource Ecology and Management, Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University, Stillwater, OK, "A bird on the edge: Cerulean Warblers still breed in Oklahoma."

Katie A. Chmielowiec, Department of Biology, Canisius College, Buffalo, NY, David F. Brinker, Heritage and Biodiversity Conservation Programs, Maryland Department of Natural Resources, Annapolis, MD, and H.

David Sheets and Sara R. Morris, Departments of Physics and Biology, Canisius College, Buffalo, NY, "Age-related differences of Northern Saw-whet Owls during fall migration in a coastal region."

Megan J. Fitzpatrick, Ashley M. Gardner, Douglas W. White, and E. Dale Kennedy, Biology Department, Albion College, Albion, MI, "Nest structure, incubation, egg viability, and sex ratio in Tree Swallows in Michigan."

Marcy Heacker, Feather Identification Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C., "What's for dinner? Feather identification of prey remains from the New Mexico ridge-nosed rattlesnake (*Crotalus willardi obscurus*)."

J. Heinen and T. O'Connell, Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, "Species turnover during autumn migration in a suburban avian assemblage."

Jason Hill, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, "Preliminary analysis of post-fledging movements of female and fledgling Saltmarsh Sharp-tailed Sparrows."

Peter Jenkins, College of the Atlantic, Bar Harbor, ME, "The importance of lobster bait as food for young Herring Gulls (*Larus argentatus*)."

Liam T. Knott and Bethany K. Stephan, Canisius College, Buffalo, NY, Michael Hamilton and Robert L. DeLeon, Buffalo Ornithological Society, Buffalo, NY, and H. David Sheets and Sara R. Morris, Departments of Physics and Biology, Canisius College, Buffalo, NY, "Avian species composition in disturbed riparian environments: a study of three waterways in western New York."

Karl L. Kosciuch, Division of Biology, Kansas State University, Manhattan, KS, James W. Rivers, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, and Brett K. Sandercock, Division of Biology, Kansas State University, Manhattan, KS, "Stable isotopes identify the natal origins of a generalist brood parasite."

Amanda Kuntz, Sara Kassmann, Kara Fedors, and Kristi Hannam, Department of Biology, SUNY, Geneseo, NY, "Non-vocal begging signals in the House Wren (*Troglodytes aedon*)."

Michaela Martin, Kathy Martin, and Alaine Camfield, Center for Applied Conservation Research, University of British Columbia, Vancouver, BC, "The ecology of alpine breeding Savannah Sparrows."

Adrian P. Monroe, Rebecka L. Brasso, and Daniel A. Cristol, Department of Biology, College Of William and Mary, Williamsburg, VA, "Occurrence of double clutching in a southern Tree Swallow population."

Dana I. Moseley, David C. Lahti, and Jeff Podos, University of Massachusetts, Amherst, MA, "Experimental test of the function of trill rate in Swamp Sparrows."

James R. Philips, Math/Science Division, Babson College, Babson Park, MA, "Mitey owls."

V. Ravinder Reddy, AINP on Agricultural Ornithology, ANGRAU, Rajendranagar, Andhra Pradesh, India, "Preference of host plants for nesting by the Baya Weaver bird, *Ploceus philippinus* L., in the three agro-climatic zones of semi-arid Tropical Andhra Pradesh, India."

Maura F. Hanna, Department of Biology, Canisius College, Buffalo, NY, Richard Keith and Brenda Keith, Kalamazoo Nature Center, Kalamazoo, MI, and H. David Sheets and Sara R. Morris, Departments of Physics and Biology, Canisius College, Buffalo, NY, "A study of age- and sex-related morphological differences in Gray Catbirds."

Nancy Rotzel, Carla Dove, and Marcy Heacker, Feather Identification Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C., "Comparing two extraction methods for DNA identification of birdstrike remains."

Amanda B. Stockwell, Department of Biology, Canisius College, Buffalo, NY, Richard Keith and Brenda Keith, Kalamazoo Nature Center, Kalamazoo, MI, and H. David Sheets and Sara R. Morris, Departments of Physics and Biology, Canisius College, Buffalo, NY, "Does age have an effect on migration? A study of the stopover ecology of the Tennessee Warbler in Michigan."

Julia Wilkinson, Department of Biology, Framingham State College, Framingham, MA, and J. Michael Reed and L. Michael Romero, Department of Biology, Tufts University, Medford, MA, "Stress during molt does not affect feather degradation via bacteria."

K. Wolfe, M. A. Voss, C. Bradshaw, K. Craig, and I. Mohar, School of Science, Penn State Erie, Behrend College, Erie, PA, "The effect of urban noise on breeding behavior and reproductive success in songbirds."

Nathan J. Zalik and Allan M. Strong, The Rubenstein School of Environment and Natural Resources, The University of Vermont, Burlington, VT, "Effects of agricultural management on breeding Savannah Sparrows mediated through food availability."

ATTENDANCE

ARIZONA: *Tucson*, Clait E. Braun.

CALIFORNIA: *Santa Barbara*, Jim Rivers.

COLORADO: *Denver*, Stephanie Jones; *LaPorte*, James A. Sedgwick.

CONNECTICUT: *Storrs*, Chris Elphick, Jason Hill; *Willimantic*, Trina Bayard.

DELAWARE: *Newark*, Bill Brown.

FLORIDA: *Ft. Myers*, Bette J. S. Jackson, Jerome A. Jackson, Steven Brent Jackson; *Lake Placid*, Reed Bowman.

ILLINOIS: *Champaign*, Ron Larkin.

INDIANA: *Notre Dame*, Doris Watt; *South Bend*, Melinda Clark.

KANSAS: *Hays*, Greg Farley.

MASSACHUSETTS: *Amherst*, Kara Belinsky, Ana Gabela, David Lahti, Dana Moseley; *Andover*, Dana Duxbury-Fox, Bob Fox; *Arlington*, Marj Rines, Bob Stymeist; *Ashland*, Julia Wilkinson; *Bradford*, David Larsen; *Braintree*, Shawn Carey; *Cambridge*, Carolee Caffrey, Jay Shetterly, Heather Shull, Brooke Stevens, Paul Ware, Fred Wasserman; *Chilmark*, Allan R. Keith; *Concord*, Peter Alden, David Lange, Julia Yoshida; *East Falmouth*, William E. Davis Jr.; *Hadley*, Alex Hoar; *Hanson*, Betty Petersen, Wayne Petersen; *Lexington*, Chris Floyd, Norma Floyd, Soheil Zendeh; *Lincoln*, Taber Allison, Linda Cocca, Nancy Soulette; *Mashpee*, Peter Trimble; *Medford*, Luke Butler, David DesRochers, Brian G. Tavernia; *Middleboro*, Kathleen S. Anderson, Andrew P. Brissette; *Milton*, Patty O'Neill; *Northampton*, Tom Litwin; *Plymouth*, Stephen Brown, Trevor Lloyd-Evans; John Kricher; *Shelburne Falls*, David Hof; *Turners Falls*, Benjamin Taft; *Watertown*, David Morimoto; *Wellesley*, Carolyn Marsh, John Marsh, James Philips.

MARYLAND: *Oxon Hill*, Paul Baicich.

MAINE: *Bar Harbor*, John Anderson, Peter Jenkins, Scott Swann; *Fairfield*, Louis Bevier; *Orono*, Stephen Agius, Steve Campbell, Kristen Covino, Rebecca Holberton, Wesley A. Wright; *Waterville*, Herb Wilson.

MICHIGAN: *Albion*, Megan Fitzpatrick, David Goodyear V, Dale Kennedy, Douglas White; *Ann Arbor*, Laura Payne, Robert B. Payne, Coral Wolf; *Chelsea*, Janet Hinshaw, Stephen H. Hinshaw.

MISSISSIPPI: *Mississipi State*, Brice B. Hanberry.

NORTH CAROLINA: *Asheville*, Louise (Lou) Weber; *Cherry Point*, Michael Begier.

NEW HAMPSHIRE: *Concord*, Pamela Hunt, Rebecca Suomala; *Gilsum*, Mary Wright; *Nashua*, David Deifik; *North Hampton*, David Donsker; *Plainfield*, Peter Stettenheim; *Stratham*, Dennis Abbott.

NEW JERSEY: *Cape May Court House*, Kevin Karlson, David Mizrahi; *Flemington*, Michael C. Allen; *Haddon Heights*, Joshua LaPergola; *Randolph*, John A. Smallwood, Mary Anne Smallwood, Nathan Smallwood.

NEW MEXICO: *Albuquerque*, Carol Lewis, John Serles; *Las Cruces*, Cara Joos.

NEW YORK: *Bowmansville*, Bethany Stephan; *Bronx*, Paul Doherty; *Buffalo*, Peggy E. Buckley, Katie Chmielowiec, Maura Hanna, Liam Knott, H. David Sheets, Amanda Stockwell; *Fredonia*, Elise Ruby; *Genesco*, Sara Kassman, Kristi Hannam; *Grand Island*, Elizabeth Morris, Sara R. Morris; *Ithaca*, William Evans, John Fitzpatrick, Alan Poole, David Winkler; Judith McIntyre, Pat McIntyre; *Webster*, Amanda Kuntz.

OHIO: *Cincinnati*, Jack Stenger; *Delaware*, Edward H. Burtt Jr., Dana Owen, Ashley M. Peele, Lauren Smith; *New Concord*, Adam Cirone, Jim Dooley, Danny Ingold; *Sandusky*, Robert C. Beason.

OKLAHOMA: *Norman*, Douglas W. Mock; *Stillwater*, Vince Cavalieri, Jason Heinen, Tim O'Connell; *Tahlequah*, Mia Revels.

PENNSYLVANIA: *Allentown*, Daniel Klem Jr., Peter G. Saenger; *East Stroudsburg*, Terry Master; *Erie*, Casey Bradshaw, Margaret Voss, Kala Wolfe; *Malvern*, Jacob Armiger; *Union City*, Katrina Craig; *Villanova*, Bob Curry, Jennifer Mortensen.

RHODE ISLAND: *Barrington*, Steven E. Reinert; *Kingston*, Susan B. Smith, Linda Vanderveer; *Newport*, Jameson Chace; *Providence*, Susan Vancura; *Warwick*, Christine Caron.

SOUTH CAROLINA: *Clemson*, Carroll Belser, Paul J. Champlin, Sidney A. Gauthreaux; *Columbia*, Austin Hughes; *New Ellenton*, Mark Vukovich.

TEXAS: *Houston*, Daniel M. Brooks; *Huntsville*, Guadalupe Quiroz; *Sherman*, Wayne Meyer, Kim Snipes.

VIRGINIA: *Alexandria*, Richard C. Banks; *Blacksburg*, Jeffrey Walters; *Charlottesville*, Janice Zimmerman, John L. Zimmerman; *Shipman*, Allen Hale; *Williamsburg*, Ruth A. Beck, Anne Condon, Scott Friedman, Andy Glass, Kelly K. Hallinger, Mikaela G. Houre, Adrian Monroe.

VERMONT: *Colchester*, Nate Zalik; *Dorset*, Elizabeth F. Gilbert.

WASHINGTON: *Seattle*, Erin Hagen.

WASHINGTON, D.C.: Carla Dove, Marcy Heacker, Nancy Rotzel.

ARMENIA: *Yerevan*, Karen Aghababyan.

CANADA, BRITISH COLUMBIA: *Vancouver*, Kathy Martin; MANITOBA: *Winnipeg*, Spencer G. Sealy; ONTARIO: *Kanata*, Erica Dunn; *Ottawa*, Rhonda Millikin; *Toronto*, James D. Rising; QUEBEC: *Ste Foy*, Jean-Pierre Savard.

INDIA: *Hyderabad*, Dr. Ravinder V. Reddy.

REVIEWERS FOR VOLUME 119

Reviewers are the lifeblood of a journal, as editors depend on them to help identify manuscripts with merit and offer suggestions to improve the data analysis, overall science, and writing. These individuals receive little recognition, but are extremely important in the process of improving the science and quality of what is published. We thank all of those listed below who served as referees for manuscripts processed (accepted and published, withdrawn, or rejected) after 1 July 2006 through completion of the December 2007 issue of Volume 119. Those shown in **boldface** reviewed more than one manuscript. The Wilson Ornithological Society and the editorial staff are indebted to and thank each person who served as a reviewer.—Clait E. Braun, Editor.

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The Wilson Journal of Ornithology 119(4):801–825, 2007

Index to Volume 119, 2007

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This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Nomenclature follows the AOU Check-list of North American Birds (1998). Reference is made to books reviewed and announcements as they appear in the volume.

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NO. 1—5 MARCH 2007
NO. 2—6 JUNE 2007
NO. 3—11 SEPTEMBER 2007
NO. 4—27 DECEMBER 2007

CONTENTS OF VOLUME 119

NUMBER 1

MAJOR ARTICLES

SHORT COMMUNICATIONS

NUMBER 2

MAJOR ARTICLES

SHORT COMMUNICATIONS

NUMBER 3

MAJOR ARTICLES

SHORT COMMUNICATIONS

NUMBER 4

MAJOR ARTICLES

SHORT COMMUNICATIONS

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Continued from outside back cover

SHORT COMMUNICATIONS

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 119, Number 4 CONTENTS December 2007

Major Articles

Continued on inside back cover