The Wilson Journal *of Ornithology*

Volume 118, Number 1, March 2006

Published by the
Wilson Ornithological Society

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

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THE WILSON JOURNAL OF ORNITHOLOGY

(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th St., Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Blvd., Ste. 680, Waco, TX 76710.

All articles and communications for publications should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109.

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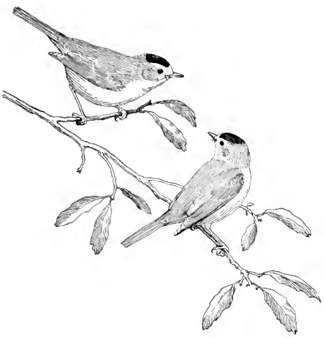
Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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

FRONTISPIECE. An adult White-masked Antbird (*Pithys castaneus*) above and a juvenile below. Previously known from only the type specimen, the species was rediscovered in 2001 in northwestern Departmento Loreto, Peru (see p. 13). Original painting (watercolor and gouache) by Daniel F. Lane.



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Published by the Wilson Ornithological Society

VOL. 118, NO. 1 March 2006 PAGES 1–130

The Wilson Journal of Ornithology 118(1):1–2, 2006

MESSAGE FROM THE EDITOR: THE NEW *WILSON JOURNAL OF ORNITHOLOGY*

This issue of your journal—118(1), March 2006—is the debut issue of *The Wilson Journal of Ornithology*. As indicated in the insert letter that came with your December 2005 issue, the Wilson Council, Wilson Society officers, and I spent considerable time over the last year debating—and eventually agreeing on—the need to update the journal's name and appearance. We believe that the new name maintains the tradition of honoring Alexander Wilson, more clearly reflects the journal's theme and content, and is more contemporary. In addition to the new journal name, the front and back covers have been redesigned, the title page is new, and we have added a new feature to *The Wilson Journal of Ornithology*.

The front cover of each issue will portray a different illustration of one of the species named after Alexander Wilson. Pen and ink or halftone artwork was solicited from over two dozen artists, and we selected those illustrations that we believe demonstrate both ornithological and artistic merit. The Wilson's Snipe on the March cover is a halftone by artist Scott Rashid. Pen and ink illustrations of the Wilson's Phalarope, Wilson's Plover, and Wilson's Storm-Petrel will appear on the covers of the June, September, and December issues, respectively. The fifth species named after Alexander Wilson, Wilson's Warbler, will appear on the cover of each issue in a logo designed by George Miksch Sutton, and the Wilson's Warblers that appeared on the cover from 1962 to 2005—also by G. M. Sutton—will now appear on the title page of the first article in each issue.

The back cover (Contents) has also been redesigned, to make it more aesthetically pleasing and easier to read. A new feature, "Once Upon a Time in American Ornithology," debuts, as well. This feature will put forward the observations and reflections of naturalists from times past—to afford retrospection and to remind us all of the exhilaration that comes from being afield and how it once was in American ornithology. I encourage Wilson Ornithological Society members and other readers of the journal to submit favorite historical field accounts (including a brief introductory statement) for consideration of publication in a future issue.

I realize that such cosmetic modifications will have little long-term effect on subscriptions, membership, or the ornithological science offered in *The Wilson Journal of Ornithology*. Combined with a renewed commitment and more substantive changes behind the scenes, however, I believe that the publication of this issue does mark a new beginning for the Wilson Ornithological Society and its journal: (1) the journal has been published on time beginning with the June 2005 issue, (2) most authors are receiving an initial decision on their work within 3–4 months, (3) the time from manuscript submission to publication now averages only about 12 months, and (4) manuscript submissions are up >20% from 2004. I sincerely hope that you, the readers and authors, welcome the new look and the improvements we continue to make to *The Wilson Journal of Ornithology*. I thank Wilson Council and officers; Keith Parsons, Karen Ridgway, and the graphics department at Allen Press; Teri Kman; and *The Wilson Journal of Ornithology* Editorial Office staff—Beth Dillon, Alison Goffredi, and Cynthia Melcher. All were instrumental in the execution and realization of the new design changes and in helping to bring *The Wilson Journal of Ornithology* back on schedule.—James A. Sedgwick, Editor.

The Wilson Journal of Ornithology 118(1):3–12, 2006

VARIATION IN MASS OF FEMALE PROTHONOTARY WARBLERS DURING NESTING

CHARLES R. BLEM[1,2,3] AND LEANN B. BLEM[1,2]

ABSTRACT.—Over an 18-year period (1987–2004), we examined variation in body mass of female Prothonotary Warblers (*Protonotaria citrea*) captured throughout their nesting cycle. As is typical for many small passerine birds, body mass was greatest during egg laying and decreased throughout incubation and feeding of young. Mass decreased significantly between the onset of incubation and fledging of both first and second broods. Mass loss was gradual during incubation, noteworthy during the first 2 days of feeding nestlings, but did not continue to decrease throughout the feeding period. Mass lost while raising the first brood was regained before initiating the second brood. Mass of female warblers, adjusted for effects of nest attempt, year, clutch size, and day and stage of nesting, increased slightly with age. Body mass of nesting female warblers varied significantly with day of the nest cycle during incubation but not during egg laying or feeding of young. Mass was associated with clutch size during incubation in both first and second broods, but was not associated significantly with brood size when females were feeding nestlings. Frequency of food delivery to nestlings was associated negatively with female body mass. Females typically made more feeding trips per day than males. Feeding rates were correlated among pairs; that is, females with higher rates of delivery were mated to males that made a higher number of trips. *Received 18 February 2005, accepted 21 October 2005.*

Mass loss is often used as an index of reproductive costs in birds (see review in Merkle and Barclay 1996), largely because it is a consistent factor in patterns of avian life history. During the breeding season, female passerine birds typically gain mass in the period before egg laying, maintain or gradually lose a small amount during incubation, and then lose a significant amount of mass during brooding (e.g., Ricklefs 1974; Freed 1981; Moreno 1989a, 1989b). A similar pattern of change during breeding has been documented in several passerine birds (e.g., Freed 1981, Ricklefs and Hussell 1984, Hillström 1995, Merilä and Wiggins 1997). Researchers have hypothesized that mass loss may be a proximate response to energetic demands (e.g., Nice 1937, Hussell 1972, Askenmo 1977). Specifically, mass loss should be greatest during periods when energy demands are greatest, particularly near fledging when nestlings have acquired the ability to thermoregulate, and are relatively large. According to this hypothesis, mass loss should be a function of brood size. A second hypothesis suggests that decreased mass reduces the energy required for flight when food demands of nestlings are greatest, thus reducing energy requirements of females and increasing the efficiency of feeding the young (e.g., Freed 1981, Norberg 1981, Hinsley 2000). In this instance, body mass should decrease shortly after eggs hatch and should be independent of brood size. A final hypothesis is that mass loss results from degeneration of female reproductive tissues during the nesting cycle (Ricklefs 1974, Ricklefs and Hussell 1984), and should not progressively occur during incubation or feeding of young. Some studies have eliminated the tissue degeneration hypothesis because gonadal atrophy is over before the period when mass loss is greatest (Moreno 1989a, 1989b; Merkle and Barclay 1996). It is difficult to isolate these three hypotheses, however, and some researchers have not found them to be mutually exclusive (e.g., Hillström 1995, Merilä and Wiggins 1997).

The question that usually has been addressed is: "Is mass loss evidence of energy demand and/or does it reduce costs of flight and enhance parental fitness?" It has been shown that energy expenditure is related significantly to rates of nest visitation, but not always in a linear manner (Bryant 1988). Furthermore, decreased body mass of adults rearing young may enhance their fitness through reduction of energy demand during the period of feeding nestlings. Our study examined

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measurements of body mass of female Prothonotary Warblers (*Protonotaria citrea*) obtained over an 18-year period. With these data, we attempted to answer three questions: (1) How does female body mass in this species vary over the breeding season? (2) Does body mass vary significantly among stages of nesting and among years? (3) What are the roles of brood size, stage of reproduction, and nest attempt in determining body mass in this species?

METHODS

Study area and measurement of mass.—Beginning in March 1987, we placed wooden nest boxes along tidal creeks in swamp forest on and near Presquile National Wildlife Refuge (37° 20′ N, 77° 15′ W) near Hopewell, Virginia (Blem and Blem 1991, 1992, 1994). The dominant tree species were black gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), and ash (*Fraxinus* sp.). Tidal amplitude in the swamp during spring tides was >1 m. Nest boxes were placed on metal poles at approximately 100-m intervals along creek banks. Box dimensions were 28 L × 9 W × 6 D cm and the entrance hole was 3.8 cm in diameter (see Blem and Blem 1991). We determined optimal nest-box sites during the first 2 years of the study (Blem and Blem 1991) and boxes were adjusted accordingly to maximize their usage by warblers. The number of nest boxes used in the study was gradually increased from 141 in 1987 to 320 in 2004.

The contents of boxes were documented 6–20 times during the breeding season each year, depending upon the demands of other investigations of reproductive output. Females were captured as they exited nest boxes, weighed to the nearest 0.1 g on a portable electronic balance, and banded with federal bands. No warbler in these analyses was weighed twice per stage, and usually not more than once during the same nest attempt. Midday (10:00–14:00 EST) masses (g) did not vary significantly with time of day (mass = −0.04 hr + 16.3, $P = 0.49$, $R^2 = 0.008$, $n = 2{,}124$). Only midday masses were used in the following analyses. We recorded dates of first eggs and clutch sizes for those nests visited often enough that we could be certain of the timing. Clutch size throughout the study was considered to be the number of eggs present at the onset of incubation. We converted first egg (nest start) dates into Julian days for analysis. Prothonotary Warblers generally produce two clutches each season (Petit 1989), and second clutches typically include fewer eggs (Blem et al. 1999). We therefore divided nests with eggs in two groups—"first nests," in which first eggs were laid from 25 April through 20 May, and "second nests," in which first eggs were laid after 20 May (see Petit 1989). Some of the second nests may have been replacement clutches for first nests that had been depredated, but we are certain that many of them were produced by females that had successfully fledged young (Podlesak and Blem 2001, 2002). We used 20 May as the separation date because it represents a major hiatus in laying and is the date after which few first clutches have been laid at our study site. It also was used because of the length of time necessary for Prothonotary Warblers to complete one nesting cycle (approximately 27 days) after a mean potential starting date of 24 April (Blem and Blem 1992). We divided nesting into three phases: laying (and egg formation), incubation, and feeding young. The first phase ended with the first day of incubation and included birds that were building nests as well as laying eggs. The second phase began with the first egg and ended with hatching (Fig. 1).

Feeding visits.—In 2002, we recorded feeding visits by warblers at individual boxes during first broods by means of battery-powered remote video cameras with programmable, portable videocassette recorders. We obtained >500 hr of nest-activity records at eight nests (four broods of three young and four broods of five young) on days 7 through 10. Video cameras were small and camouflaged and did not noticeably alter behavior of the warblers. Individual visits (see Figs. 2–3) were transcribed from replays of the recordings in the lab. We totaled all feeding visits made by both parents from dawn-to-dark for all 4 days. We could not accurately assess prey size from the recordings, but we did count the number of items—mostly caterpillars—that were distinctly larger than 2 cm ("large prey"), as judged by the entry hole in the nest box. Female warblers were weighed 2 days before nestlings fledged.

Analyses.—Over the 18-year period, we obtained 2,124 measurements of body mass from

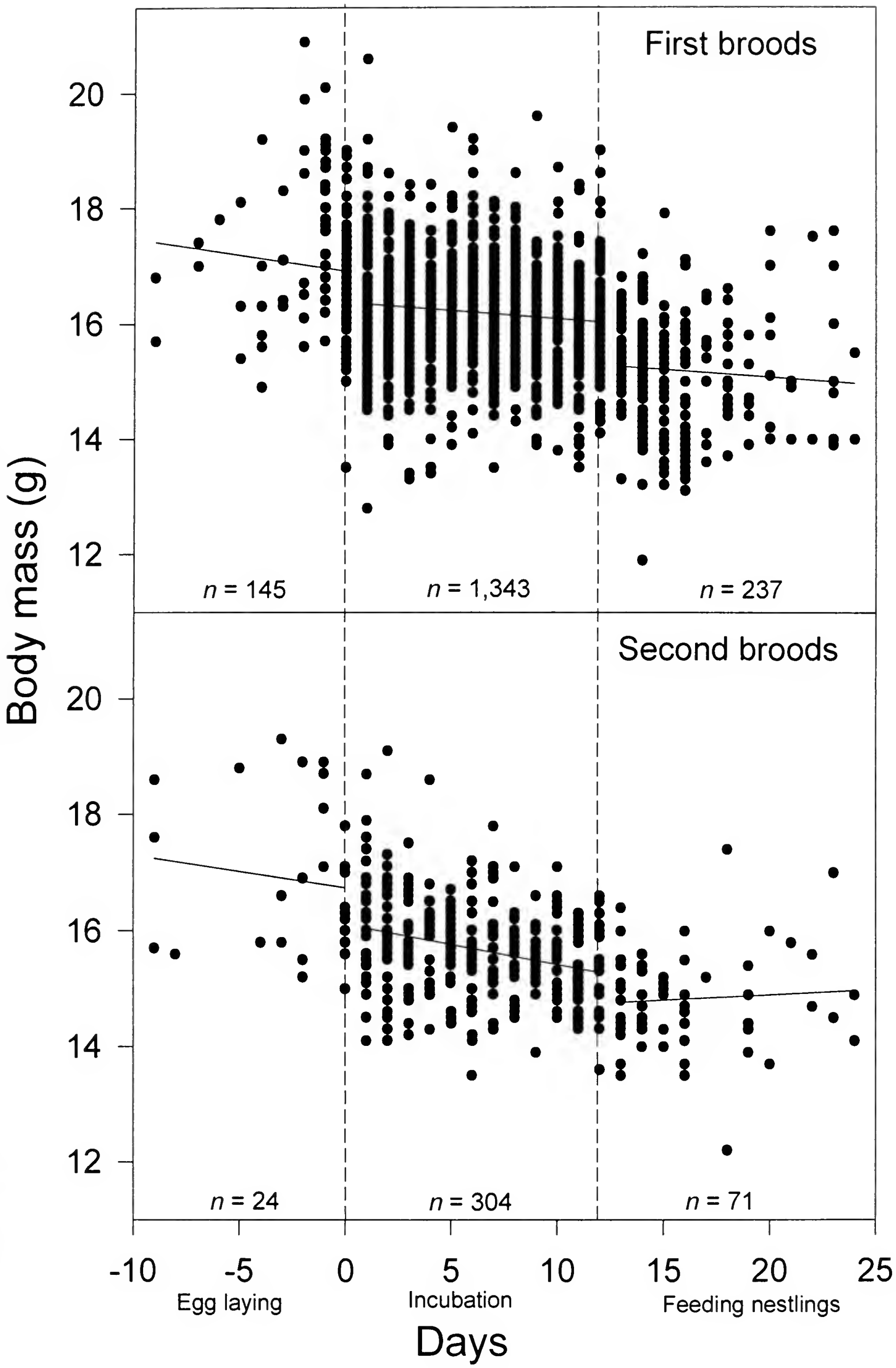

FIG. 1. Body mass (g) of female Prothonotary Warblers during nesting in eastern Virginia, 1987–2004 (day 0 = first day of incubation). Numerous circles are hidden under duplicate values (*n* = 2,124).

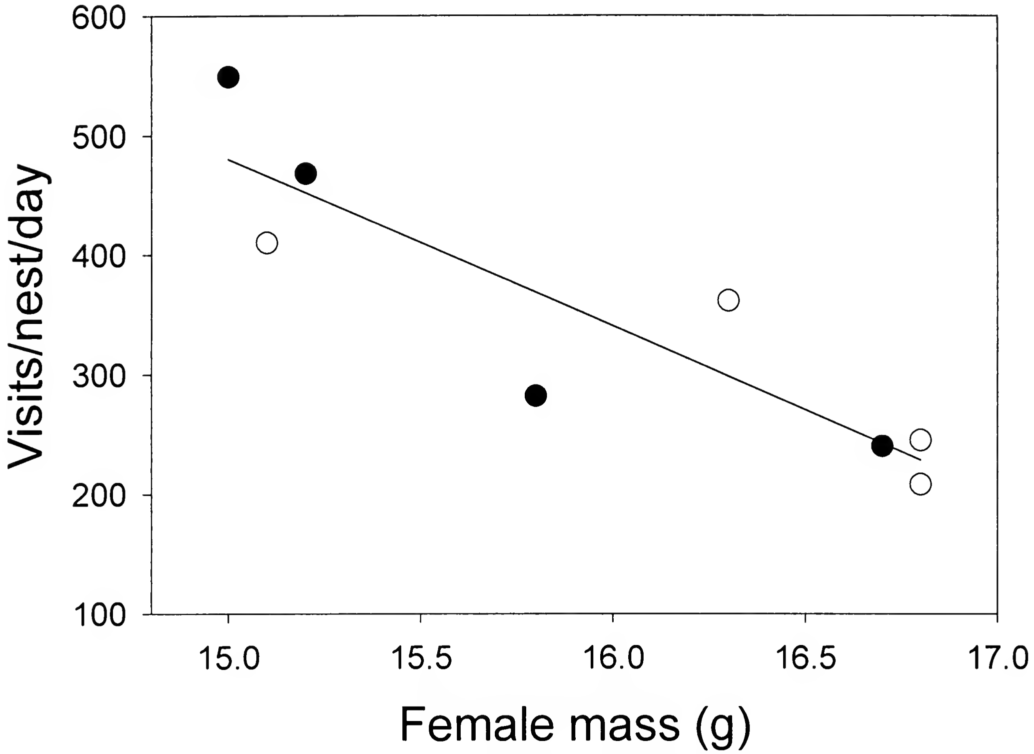

FIG. 2. Feeding visits/nest/day made by female Prothonotary Warblers during days 7–10 of feeding nestlings versus female body mass at the end of incubation, eastern Virginia, 2002. Open circles represent broods of three nestlings; solid circles represent broods of five nestlings. Nest visitation was a function of female body mass, regardless of brood size.

977 different adult female warblers. For analysis, we partitioned these measurements among nesting attempts (first and second nests, n = 1,344 and 780, respectively) and stages of nesting (egg formation and laying, incubating, and feeding). The number of measurements in each stage-year combination varied from 24 during laying in second nests to 1,344 during incubation in first nests. Clutch size varied from two to six eggs and ages of females ranged from 1 to 8 years.

To examine differences in mass between nests and among stages of nesting and brood sizes (adjusted for day of nesting), we used univariate ANCOVA with multiple independent variables in PROC GLM (SAS Institute, Inc. 2000). Brood size, nest attempt, age, stage of nesting, and their interactions were considered fixed (categorical) effects in various models. Day of nesting (range = −9 to 24; 0 = day of onset of incubation) was a continuous variable. Analysis of covariance was done using the PROC GLM procedure because the data set was unbalanced among effects (Zar 1999). Type III sums of squares were used, adjusting significance of each factor for the effects of all other variables. Single comparisons of means were done by means of appropriate t-tests based on tests of equality of variances (SAS Institute, Inc. 2000). Few females were measured more than once during the same stage of nesting in a given nest in the same year; therefore, we did not use repeated measures analyses. Because some of the associated variables were not measured with each measurement of body mass, sample sizes vary among analyses. All t-tests were two-tailed. Means are presented ± SD. Statistical significance was set at $P < 0.05$.

RESULTS

Body mass.—In the following analyses and comparisons, we assumed that patterns found between specific points along a regression

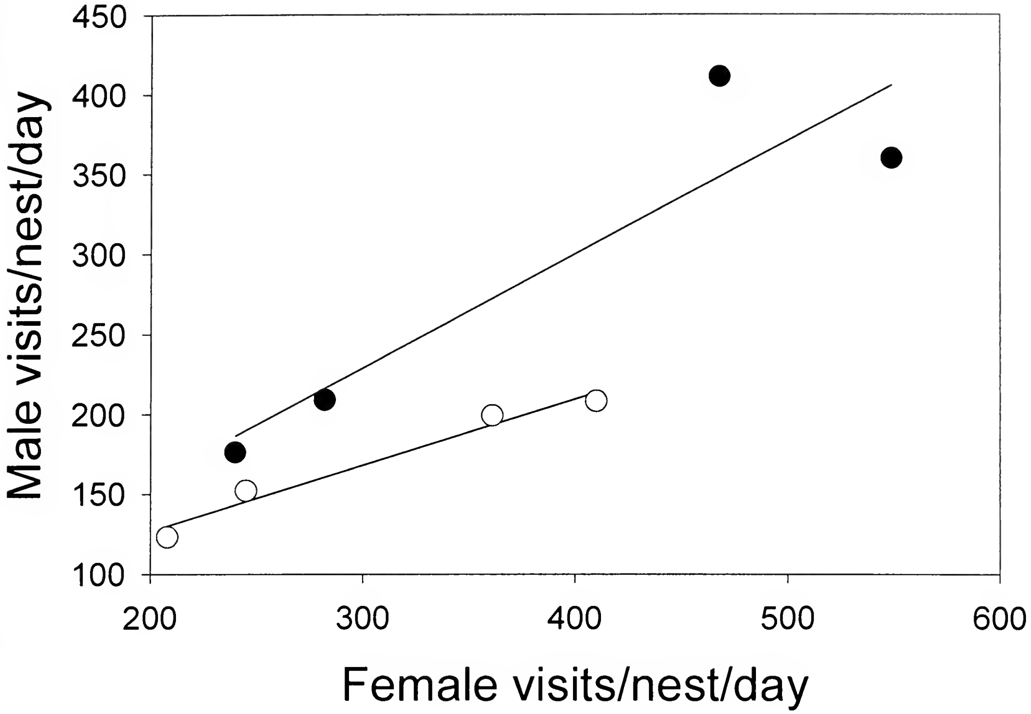

FIG. 3. Feeding visits/nest/day by mated pairs of Prothonotary Warblers during days 7–10 of feeding nestlings, eastern Virginia, 2002. Open circles represent broods of three nestlings; solid circles represent broods of five nestlings. Males brought food less often than females, but the frequency of male visits/nest/day was a function of that of females.

were representative of patterns deduced from single measurements of numerous females. This was confirmed in our observations of multiple measurements of a few single females (CRB unpubl. data).

Body mass of female Prothonotary Warblers varied over the breeding season in the typical passerine pattern. That is, variation was greatest during egg laying, mass decreased gradually during incubation, and then there was a noteworthy decrease in mass immediately after the eggs hatched (Fig. 1). After the decline immediately after hatching, adult female mass did not change over time throughout the period of feeding nestlings. Mean body masses did not differ between nest attempts during egg formation and laying (first nests: 16.9 ± 1.2, $n = 143$; second nests: 16.8 ± 1.9, $n = 93$, $F_{1,235} = 0.20$, $P = 0.65$), but did differ between nests during incubation (first nests: 16.2 ± 0.9, $n = 1{,}225$; second nests: 15.6 ± 0.9, $n = 304$, $F_{1,1526} = 6.7$, $P = 0.011$) and during the feeding phase (first nests: 15.2 ± 1.0, $n = 238$; second nests: 14.9 ± 0.8, $n = 121$; $F_{1,358} = 6.7$, $P = 0.012$). Mass did not vary with day of nesting in the laying or feeding stages of either nesting attempt, but it did decline significantly with day of incubation (first nests: $F_{1,1342} = 18.0$, $P < 0.001$; second nests: $F_{1,303} = 33.5$, $P < 0.001$).

As judged by the collective scatter of individual masses over time, females collectively lost 10.1% of their body mass between the onset of incubation and fledging of first broods and 11.3% in second broods. Much of this loss appeared to occur during the first 2 days of feeding nestlings (5.4 and 7.7%, respectively). Mass lost during first broods was regained before the initiation of second broods. Body mass extremes were 11.9 g for an incubating bird and 21.0 g for a female during the early days of egg laying.

When the data set including all variables was considered ($n = 1{,}814$; Fig. 1), mass varied significantly with nest attempt, stage of nesting, clutch size (2–6), female age (1–8

TABLE 1. Analysis of covariance of body mass of female Prothonotary Warblers in eastern Virginia, 1987–2004 (n = 1,814). All two-way and three-way interactions were statistically insignificant except for nesting attempt × stage of nesting. Clutch sizes were 2–6 and ages were 1–8 years. Days of nesting ranged from −9 through 24.

Source	df	F	$P > F$
Nesting attempt	1	7.6	0.006
Stage of nesting	2	27.0	<0.001
Clutch size	4	10.4	<0.001
Age	5	6.8	<0.001
Day of nest cycle	1	35.7	<0.001
Year	17	2.6	0.015
Nesting attempt × stage of nesting	1	2.8	0.050

years), day of the nest cycle, and year (Table 1). There was a significant interaction between nesting attempt (first/second nest) and stage of nesting, but no other two-way and three-way interactions were statistically significant. When stages of nesting were analyzed individually, body mass during the laying and feeding stages did not differ among clutches/broods of different sizes and mass did not vary significantly with day of nesting in these stages.

Body mass adjusted for effects of nest attempt, year, clutch size, and day and stage of nesting varied significantly with female age ($F_{1,2213}$ = 15.0, P < 0.001; Table 2). Unadjusted masses indicated that much of this change occurred between birds in their first year (SY birds) and all older age classes (ASY). Measurements of mass were obtained from a large range of ages, including 64 measurements that exceeded the published maximum age (5 years 11 months) for the species (Kennard 1975).

During incubation, mass was significantly associated with day of nesting and clutch size (Table 3). Mass tended to decrease gradually throughout incubation. Birds with larger clutches during first nesting attempts tended to have greater body mass; birds with small clutches in second nests had the lowest body mass.

Feeding visits.—Total nest visits per day made by females during days 7–10 of feeding nestlings was a function of female body mass, regardless of brood size (three young: $F_{1,3}$ = 13.8, P = 0.023, R^2 = 0.80; five young: $F_{1,3}$ = 15.5, P = 0.034, R^2 = 0.85; Fig. 2). Males brought food less often than females (three young: χ^2 = 38.2, df = 1, P < 0.052; five

TABLE 2. Least-squares means of body mass among incubating female Prothonotary Warblers during mid-incubation (days 3–8) as a function of age (years) in eastern Virginia, 1987–2004 (n = 1,540). All means were adjusted for the effects of nest attempt, clutch size, and day and stage of nesting.

Age	Mean mass (g)	n
1	16.0	275
2	16.3	565
3	16.4	420
4	16.4	147
5	16.1	80
≥6	16.1	48

TABLE 3. Analysis of covariance of body mass among female Prothonotary Warblers in eastern Virginia, 1987–2004 by stage of nesting (n = 2,124 in all analyses). Clutch and brood sizes were 2–6 and ages were 1–6 years; days of nesting ranged from −9 through 24 (day 0 = first day of incubation).

Source	df	F	$P > F$
Egg formation and laying (n = 169)			
Nesting attempt	1	0.9	0.34
Clutch size	4	2.2	0.092
Day of nesting	1	0.2	0.70
Age	5	1.7	0.13
Incubation (n = 1,647)			
Nesting attempt	1	52.3	<0.001
Clutch size	4	9.3	<0.001
Day of nesting	1	40.4	<0.001
Age	5	6.3	<0.001
Feeding nestlings (n = 308)			
Nesting attempt	1	4.3	0.039
Brood size	4	1.0	0.45
Day of nesting	1	0.3	0.58
Age	5	1.3	0.26

TABLE 4. Mean visitation rates (no./day ± SD) of male and female Prothonotary Warblers (percent of total) for days 7–10 of nestling development in eastern Virginia, 2002.

	Female visits		Male visits	
Brood size	Per nest	Per nestling	Per nest	Per nestling
3 (n = 4)	306 ± 95 (63.8)	102.0	171 ± 40 (36.2)	57.0
5 (n = 4)	396 ± 148 (56.5)	79.2	295 ± 108 (43.5)	59.0

young: $\chi^2 = 12.1$, df = 1, $P < 0.054$; Table 4), but frequency of male visits per day was a function of that of females (female visits = 1.0 ± 1.06 × male visits; $R^2 = 0.75$, $F_{1,3} = 17.7$, $P = 0.006$; Fig. 3). Female feeding trips per nestling decreased with brood size ($\chi^2 = 9.3$, df = 1, $P < 0.05$; Table 4), but male trips per nestling did not decrease ($\chi^2 = 0.034$, df = 1, $P > 0.05$). The percentage of total parental visits made by males declined from a high of 44.0% on day 7 to a low of 34.8% on day 10. Males brought significantly more "large prey items" to the nest than did females (males: 330, females: 210; $\chi^2 = 26.7$, df = 1, $P < 0.05$). These prey items were mostly *Hexagenia* sp. mayflies and lepidopteran caterpillars. There was no significant difference in the number of larger prey delivered by males to different brood sizes (175 in broods of three, 155 in broods of five; $\chi^2 = 1.2$, df = 1, $P > 0.05$).

DISCUSSION

Body mass clearly is associated with stage of breeding activity in small passerines (Freed 1981, Ricklefs and Hussell 1984, Cichon 2001), and each stage—egg formation and laying, incubation, and feeding of nestlings—is characterized by a different pattern of mass change (e.g., Fig. 1). Mass change of female Prothonotary Warblers in our study was similar to that reported in several other studies of passerine species (e.g., Freed 1981, Ricklefs and Hussell 1984, Johnson et al. 1990, Hillström 1995). During egg laying, body mass varied greatly with follicle formation and release of eggs, then declined progressively throughout incubation (Fig. 1), and dropped sharply at hatching. Female mass then remained relatively constant throughout the period of feeding nestlings. Mass changes in Prothonotary Warblers during egg laying and incubation were similar to those of all small passerines and require little explanation. Mass loss at hatching is more complex and differs among species. Because the significance of this loss is uncertain, the behavior and compositional dynamics of females requires closer scrutiny.

Two potential hypotheses have been proposed to explain mass loss of female birds during feeding of nestlings: (1) energy demand (cost of reproduction hypothesis = reserve mobilization hypothesis; Cavitt and Thompson 1997), and (2) long-term benefits from reduction of power demands for flight during feeding (mass adjustment hypothesis = flight efficiency hypothesis). Forming and laying eggs, incubating, and feeding nestlings requires additional collection and expenditure of energy, whereas adjusting mass to save energy expended in flight during the numerous trips made while feeding young is an adaptive loss.

It has become obvious that body mass can vary as a result of energy demand during extreme years (Merilä and Wiggins 1997) or with larger broods (Nur 1984). It appears to be axiomatic that reserves should be depleted during times of high-energy demand and it is well known that body mass and energy reserves are closely related (Blem 1990). Part of the variation in mass within stages of the nest cycle may result from differences in annual factors, such as temperature extremes, inclement weather (Merilä and Wiggins 1997), or brood number (De Laet and Dhondt 1989). Because of our large sample size, we were able to detect annual variation within the incubation period of first nests, largely by eliminating much of the variation associated with several other variables. Others (e.g., Johnson et al. 1990) have likewise found significant annual variations in mass of breeding birds, and extreme environmental conditions in exceptional years have important influences on body mass (Merilä and Wiggins 1997).

Not all studies, however, have shown that energy demand is an important factor in body mass. For example, larger broods are not always associated with greater mass loss of females (Pinkowski 1978, this study), even though energy expenditure by females increases with brood size (Sanz et al. 1998). Furthermore, food-supplementation studies have provided mixed results. Food supplements did not affect female mass, brood mass, or length of the nestling period among House Wrens (*Troglodytes aedon*; Cavitt and Thompson 1997) or Northern Wheatears (*Oenanthe oenanthe*; Moreno 1989a). However, food-supplemented female Mountain Bluebirds (*Sialia currucoides*; Garcia et al. 1993) maintained greater body mass and fledged larger young than females receiving no food supplementation. Some studies have found that female mass is a negative function of brood size (Nur 1984, Merilä and Wiggins 1997), and that energy demand during first broods may influence the probability of having a second brood in some species (De Laet and Dhondt 1989). In Prothonotary Warblers, it appears that many females totally recover lost mass fairly quickly between nest attempts. It has been suggested that species breeding in different environments may respond differently to stress associated with increased energy requirements and there may not be selection for adaptive mass loss (Cavitt and Thompson 1997).

The pattern of mass change in female Prothonotary Warblers in our study does not support the cost of reproduction hypothesis, but it does support the mass adjustment hypothesis. Important supporting observations included (1) the regular loss of mass after hatching in both nesting attempts, (2) the lack of influence of brood size on female mass, (3) no increasing loss in female mass as young grew and when feeding activity levels were greatest, (4) more feeding trips made by females that weighed less, and (5) little evidence that males adjusted their feeding efforts to offset demands on females. Trivers (1972) predicted that, within breeding pairs, females would provide the largest proportion of nestling care because they had a larger share of investment of energy than males. In our study, female Prothonotary Warblers made more feeding trips than males (both broods). Male Prothonotary Warblers, however, brought a greater proportion of large prey, which may have significantly offset female effort during later stages in the nesting cycle even though males made fewer trips as nestlings neared fledging.

The mass adjustment hypothesis suggests that birds benefit from mass loss due to decreased wing loading (e.g., Freed 1981, Norberg 1981, Ricklefs and Hussell 1984, Cavitt and Thompson 1997). Energy saved by mass reduction may enable parent birds to raise more young faster or produce fledglings with greater mass. Observations supporting the mass adjustment hypothesis include (1) greater loss of mass before the period of maximum energy requirement (e.g., Freed 1981, Ricklefs and Hussell 1984, Merkle and Barclay 1996, this study), (2) loss of mass independent of brood size (e.g., Freed 1981, this study) or length of incubation (Sanz and Moreno 1995, this study), and (3) no increase in body mass among food-supplemented females feeding nestlings (Cavitt and Thompson 1997). In our study, mass loss of females during incubation was correlated with clutch size, but mass of females feeding nestlings was not affected by brood size, nor did female mass decrease throughout nestling development. If increased energy demand is important, then female mass should decline significantly as nestlings grow, although it is possible that males may "pick up the slack." That is, male warblers might feed young more frequently or with higher-quality food in large broods than small, thus reducing energy demands on females and allowing them to maintain their mass and fitness. Our observations weakly support these ideas. Males did bring more large prey items than females, but this did not vary with brood size or with nestling age. Furthermore, males made fewer visits late in the nesting cycle than females. This pattern is nearly identical with that documented for Willow Tits (*Poecile montanus*; Rytkönen et al. 1996). Similar studies have shown that nest visitation rates may be greater in males of some species (Grundel 1987), greater in females of others (Pinkowski 1978, Conrad and Robertson 1993), or may not differ between the sexes (Best 1977, Knapton 1984, Omland and Sherry 1994). The significance of the age:body mass relationship during the reproductive period is not clear. We are aware of few studies that have demonstrated an age effect on mass (see De Laet and Dhondt 1989, Merilä and

Wiggins 1997). In our study, however, female age had a significant effect on body mass, even after mass was adjusted for the effects of many other variables.

Mass variation of female birds during nesting obviously is a complex phenomenon. Deeper insight into mass variations will be obtained only with studies that combine measures of body composition, condition of reproduction tracts, and measures of hormone levels with stage of nesting. While time-consuming, collecting large data sets over numerous years is well worth the trouble, but would be even more valuable if simultaneous studies could be carried out at several sites over the range of the species.

ACKNOWLEDGMENTS

We thank the officials of the Eastern Virginia Rivers National Wildlife Refuge (NWR) Complex for permission to conduct this study at Presquile NWR. The North American Bluebird Society financially supported box construction. More than 100 students, friends, and faculty colleagues assisted in this project and we thank them all, especially A. S. and K. C. Seidenberg and J. R. and R. J. Reilly for their continuous help over many years. We thank L. B. Williams, K. R. Guisinger, and D. S. Stevens for transcribing visits of warblers from long, boring tape recordings. The Virginia Society of Ornithology and several of its chapters helped fund our efforts. This is Rice Center for Environmental Life Sciences Research Contribution No. 001.

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The Wilson Journal of Ornithology 118(1):13–22, 2006

THE REDISCOVERY AND NATURAL HISTORY OF THE WHITE-MASKED ANTBIRD (*PITHYS CASTANEUS*)

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ABSTRACT.—In July 2001, a Louisiana State University Museum of Natural Science expedition rediscovered the White-masked Antbird (*Pithys castaneus*) at a site along the Río Morona in northwestern Departmento Loreto, Peru. Prior to this rediscovery, the species was known only from the type specimen, taken in 1937, and nothing was recorded concerning its natural history. The lack of additional specimens led to speculation that *P. castaneus* was a hybrid. Here, we present data demonstrating that the White-masked Antbird is a valid species, and we report the first observations of its behavior, habitat, morphology, and voice. *Received 14 January 2005, accepted 11 October 2005.*

In 1938, Berlioz (1938) described a distinctive new species of antbird in the genus *Pithys*—until then considered monotypic—from a single specimen collected by Ramon Olalla on 16 September 1937 at "Andoas, lower [Río] Pastaza, eastern Ecuador." This new species, the White-masked Antbird (*Pithys castaneus*), has remained one of the most intriguing mysteries of Neotropical ornithology for over 60 years (see David and Gosselin 2002 for gender of scientific name). Besides the collector, no biologist had ever seen the bird alive, and there is no information on the species' natural history or preferred habitat. The type locality, "Andoas," is particularly intriguing in that at least three sites in the Pastaza area bear this name (Stevens and Traylor 1983, Paynter 1993), and according to T. Mark (*in litt.*), we may never really know the true location of the type locality.

The type specimen, a male (contra Ridgely and Tudor 1994), is housed at the Paris Museum in France. According to Berlioz (1938, 1948), it was part of a collection that included three specimens of White-plumed Antbird (*P. albifrons peruvianus*) and therefore appeared to be a sympatric congener. It differed from *P. albifrons* in its larger size, its lack of any gray on the body, and its lack of elongated plumes on the face or throat.

Decades passed without any additional records of *P. castaneus*. Subsequent authors doubted the validity of the species, and many suggested that it represented nothing more than a hybrid of *P. albifrons* and another antbird species (Sibley and Monroe 1990, Schulenberg and Stotz 1991, Collar et al. 1992, Stattersfield and Capper 2000, Ridgely and Greenfield 2001b). Willis (1984) and personnel at the Philadelphia Academy of Natural Sciences (ANSP; Collar et al. 1992, Ridgely and Tudor 1994) searched without success for *P. castaneus* along the upper Río Pastaza in Peru and Ecuador, respectively.

Thus, when our Louisiana State University Museum of Natural Science (LSUMZ) ornithological field team visited several sites in northwestern Departamento Loreto, Peru, from May through July 2001, it was with great surprise that we found *P. castaneus* to be fairly common at one of our field sites. The main goal of our fieldwork was to inventory the avifauna of two isolated patches of *varillal* (white sand) forest (see Whitney and Alvarez 1998; Alvarez and Whitney 2001, 2003). One of these forest patches was in the interfluvium between the Morona and Santiago rivers in northern Peru, north of the Río Marañón, only about 60 km west of the Río Pastaza, and it was there that we found *P. castaneus*.

Remarkably, while reviewing specimen material at the Museo de Historia Natural de la Universidad Mayor San Marcos (MUSM),

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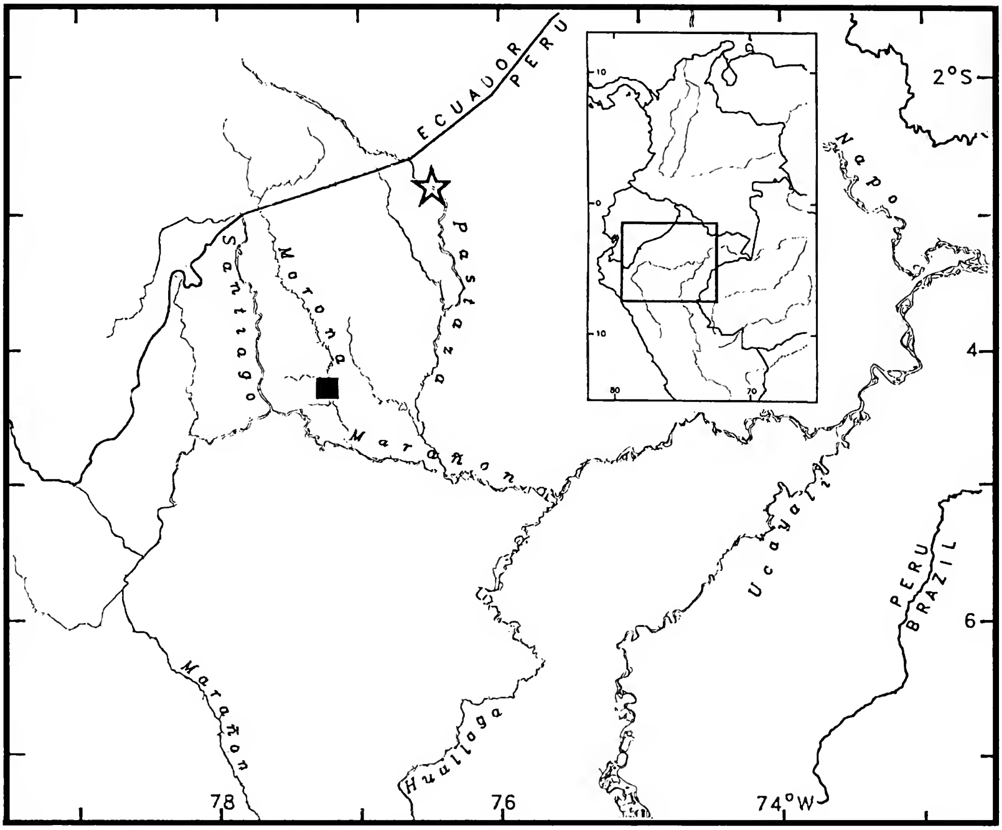

FIG. 1. Known localities for *Pithys castaneus* in northwestern Departmento Loreto, Peru. The star represents suspected location of "Andoas," the type locality, on the Río Pastaza (Berlioz 1938). The square represents the location of the species' rediscovery in July 2001 on the west bank of the Río Morona (04° 17′ S, 77° 14′ W). The Cordillera Campanquís lies between the ríos Morona and Santiago, immediately to the west of our field site.

Lima, in November 2002, we discovered two additional specimens of *P. castaneus* (one adult and one juvenile). These specimens were reportedly taken somewhere in the Cordillera Campanquís region on the border of Departmentos Amazonas and Loreto between the Morona and Santiago rivers (see Fig. 1), in the mid- to late 1990s by a Peruvian anthropologist, Andres Treneman (I. Franke J. pers. comm.). Unfortunately, no additional specimen data are available, and the collector could not be contacted for additional information.

METHODS

Locality.—We established a campsite on the west bank of the Río Morona about 54 km north-northwest of its mouth (04° 17′ S, 77° 14′ W; Fig. 1), Departmento Loreto. The study site was on the south side of the mouth of Quebrada Cashacaño, a right-bank tributary of the Río Morona, about 2.3 km north of the village of Tierra Blanca. We observed and made a general collection of birds at this site between 2 and 21 July 2001. Our camp was set up in a clearing of a homestead abandoned about 30 years earlier and which, reportedly, has been reinhabited since our visit (B. Walker pers. comm.). A preexisting trail, used for the harvest of palm fronds for thatched-roof construction, led directly into white-sand forests for about 2 km. Another trail, cut along the bluff above the Morona, connected the camp with the village of Tierra Blanca. From this trail, at least another three trails also entered the *varillal* forest. Additional trails were cut near camp for census routes and net lanes;

most trails were in *varillal,* but three also entered the adjacent *varzea* (seasonally inundated) forest. We also found two patches of richer clay-soil *terra firme* forest north and south of the surveyed *varillal* forest patch, into which we cut two trails.

Habitat.—Most of the forest where *P. castaneus* was observed—particularly away from major water bodies—grew on very moist, white-sand soils. Numerous areas of wet, swampy conditions indicated a high water table. The terrain was without significant relief, but throughout the *varillal* forest were many small depressions where water accumulated (particularly after rains), presumably pits resulting from tree-falls. The soil consisted of rather coarse sand with stones of up to 5 cm in diameter (up to 15 cm in the small creeks that transected the forest interior). Using a natural cut at the Río Morona riverbank for reference, the sandy soil is approximately 4 m deep at the river's edge. Typical of many *varillal* forests, a thick layer of dead leaves and humus covered the forest floor (Ruokolainen and Tuomisto 1993, 1998; Richards 1996). The forest canopy of the *varillal* was relatively even, with a height of about 20 to 30 m. The relative absence of buttressed trees is typical of *varillal* forests (Richards 1996); however, many such trees were present in more humid forest areas at the Morona site. As has been noted in other *varillal* forests (Anderson 1981, Richards 1996), there were few lianas, and epiphytic growth was negligible.

Data collection.—We collected specimens using mist nets and shotguns. Permits for specimen collection were issued by Peru's Instituto Nacional de Recursos Naturales (INRENA). Specimens were deposited into the collections of LSUMZ and MUSM. Skull ossification, gonad information, and presence of fat in prepared specimens were determined following standard LSUMZ specimen preparation protocol. Natural history information was acquired through opportunistic (not systematic) encounters with *P. castaneus.* Spectrograms of voice recordings were prepared using Canary sound analysis software (Charif et al. 1995).

Specimens examined.—Pithys castaneus: Peru: Loreto; west bank of Río Morona, ~54 km NNW of the mouth, 140 m elevation (04° 17′ S, 77° 14′ W) (LSUMZ 172973, 172974, 172975, 172976 [skeleton and partial skin], 172977, 172978, 172979 [skeleton and partial skin], MUSM 23504, 23505, 23506, 23507; DFL 1646 [skeleton, uncataloged], TVH 399 [alcohol, uncataloged]).

Pithys albifrons: Ecuador: Pastaza; Coconaco, 300 m elevation (LSUMZ 83237); Peru: Amazonas; Huampami, ~215 m elevation (LSUMZ 84917), Chiriaco, ~320 m elevation (LSUMZ 78514, 88018, 88019, 88022); Loreto; Libertad, S bank of Río Napo, 80 km N of Iquitos, 120 m elevation (LSUMZ 110094, 110096, 110097, 110098, 110099, 110100, 110102, 110103, 110104, 110105); 157 km by river NNE of Iquitos, N of Río Napo, 110 m elevation (LSUMZ 110106, 110109, 110112, 110113).

Gymnopithys leucaspis: Peru: Loreto; west bank of Río Morona, ~54 km NNW of the mouth, 140 m elevation (04° 17′ S, 77° 14′ W) (LSUMZ 172985); Quebrada Orán, ~5 km N of Río Amazonas, 85 km NE of Iquitos, 110 m elevation (LSUMZ 119884, 119885, 119886, 119887, 119890, 119891, 119892, 119893).

Phlegopsis erythroptera: Ecuador: Sucumbios; Limoncocha, 300 m elevation (00° 24′ S, 76° 37′ W) (LSUMZ 70916, 70917, 70919, 83314). Peru: Loreto; W bank of Río Morona, ~54 km NNW of the mouth, 140 m elevation (04° 17′ S, 77° 14′ W) (LSUMZ 173001); 1.5 km S of Libertad, S bank of Río Napo, 80 km N of Iquitos, 120 m elevation (LSUMZ 110213, 110215, 110217); 1 km N of Río Napo, 157 km by river NNE of Iquitos, 110 m elevation (LSUMZ 110219); lower Río Napo region, E bank of Río Yanayacu, ~90 km N of Iquitos, 120 m elevation (LSUMZ 115573).

Rhegmatorhina melanosticta: Peru: Amazonas; headwaters of Río Kagka (of Río Cenepa), ~790 m elevation (04° 16′ S, 78° 09′ W) (LSUMZ 88028, 88029); San Martín; ~15 km by trail NE of Jirillo on trail to Balsapuerto, 1,350 m elevation (LSUMZ 116947); Huanuco; ~35 km NE Tingo of María, Hacienda Santa Elena, ~1,000 m elevation (LSUMZ); Pasco; Abra Aguachini, ~30 km SW of Puerto Bermudez, 1,020 m elevation (LSUMZ 130274); Pasco; Puellas, km 41 on Villa Rica–Puerto Bermudez highway, 950 m elevation (LSUMZ 106073, 106074, 106078).

RESULTS

Specimen data.—We collected 13 specimens of *Pithys castaneus* during our visit to the Río Morona site. We prepared nine as study skins (from which several trunk skeletons were saved), three as complete skeletons (from which two partial skin specimens were saved), and one was preserved whole in alcohol. Mass and lengths of flat-wing, tail, tarsus, and culmen (from distal edge of the nares to bill tip) of all specimens are presented and compared with measurements of the *P. castaneus* holotype and other Peruvian ant swarm-following antbirds (Table 1).

Three of the 12 specimens in "adult" plumage (LSUMZ 172973, MUSM 23504, MUSM 23507) still possessed a bursa of Fabricius and one had an incompletely ossified skull (75% ossification), suggesting that first basic plumage is acquired quickly and is nearly indistinguishable from definitive plumage (but see below). One specimen (LSUMZ 172978) was a male still largely in juvenal plumage (skull ossification 50%, bursa 8 × 6 mm). Of the 12 specimens dissected, only 2—both with immature characters—were reported to have subcutaneous fat deposits: "trace fat" in one and "light fat" in the other. Six of 12 specimens dissected exhibited trace or light body molt. Seven individuals had asymmetrical wing molt, and seven had asymmetrical tail molt. Stomach contents were reported as "insect parts" for all specimens in which the stomachs were not empty. The guts of two specimens were infested with nematodes.

Variation in the series.—Twelve specimens—5 males and 7 females—exhibited similar plumage, with no sexual dichromatism. All these adults appeared to match the description of *P. castaneus* and the photos of the holotype very closely. Of the specimens in "adult" plumage, two that appeared to be in their first year (see above) have very sparse, light-grayish scaling on the center of the throat (unmarked white in all other individuals), suggesting that it may be an age-related character. Otherwise, plumage characters were uniform among all the "adult" specimens. The juvenal-plumaged bird differs in being washed with colder brown overall, particularly on the breast, vent, and center of the back. Furthermore, the white of the juvenile's face

TABLE 1. Mean (± SD) measurements of specimens[a] of *Pithys castaneus*, *P. albifrons*, and associated species from Peru and Ecuador.

	n	Mass (g)	Flat wing (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)
Pithys castaneus (holotype)[b]	1	—	82	—	23	15
Pithys castaneus (Morona specimens-males)	6	29.6 ± 2.7	82.8 ± 2.0	52.2 ± 1.9	25.0 ± 0	12.0 ± 0.7
Pithys castaneus (Morona specimens-females)	5	30.1 ± 1.5	80.6 ± 1.7	52.3 ± 2.9	24.4 ± 0.5	12.0 ± 1.2
Pithys albifrons (males)	10	18.7 ± 2.4	67.5 ± 2.0	36.4 ± 1.5	22.2 ± 0.7	10.9 ± 0.4
Pithys albifrons (females)	10	18.5 ± 1.3	65.5 ± 1.5	35.6 ± 1.1	21.5 ± 0.8	10.6 ± 0.4
Gymnopithys leucaspis (males)	5	23.9 ± 2.7	73.5 ± 2.3	43.9 ± 0.9	26.0 ± 0.5	11.8 ± 0.4
Gymnopithys leucaspis (females)	5	23.8 ± 2.3	71.9 ± 1.3	42.9 ± 2.1	25.8 ± 1.2	11.0 ± 0.6
Phlegopsis erythroptera (males)	5	58.4 ± 5.2	91.6 ± 1.7	63.3 ± 2.4	33.5 ± 1.7	12.9 ± 0.6
Phlegopsis erythroptera (females)	5	58.2 ± 7.0	88.0 ± 1.3	59.0 ± 1.0	32.0 ± 1.4	12.0 ± 0.5
Rhegmatorhina melanosticta (males)	4	30.0 ± 1.9	81.3 ± 5.2	53.0 ± 2.0	27.6 ± 1.2	12.4 ± 0.3
Rhegmatorhina melanosticta (females)	5	33.0 ± 4.7	78.0 ± 2.8	49.8 ± 2.5	27.4 ± 0.8	11.7 ± 0.6

[a] See section on *Specimens examined* for catalog numbers and localities of specimens.

[b] Measurements of the holotype are taken from Berlioz (1938), and are likely not to have been measured in the same way as the other specimens included here.

TABLE 2. Number of individuals per species attending army ant swarms (*Eciton burchelli* and *Labidus praedator*) with *Pithys castaneus*, Departmento Loreto, Peru, July 2001. Columns represent individual swarms. Only swarms observed for >15 min were included.

	Date (ant swarm[a])								
	4 July (E)	6 July (E)	6 July (E)	8 July (E)	10 July (L)	11 July (E)	12 July (E)	14 July (L)	17 July (E)
Pithys castaneus	2	4	3	3	1	1	4	4	3
Pithys albifrons	3	5	—	—	—	—	—	—	—
Phlegopsis erythroptera	—	2	—	—	—	—	—	—	—
Gymnopithys leucaspis	5	4	2	2	—	3	2	4	4
Hylophylax poecilinota	—	2	2	1	1	—	—	—	—
Percnostola arenarum	1	—	1	—	—	—	1	1	2
Dendrocolaptes certhia	1	3	—	—	—	—	—	—	—
Dendrocincla merula	—	—	—	—	—	—	—	1	1
Xiphorhynchus ocellatus	2	2	—	—	—	1	—	1	1
Deconychura longicauda	1	—	—	—	—	—	—	—	—

[a] E = *Eciton burchelli*, L = *Labidus praedator*.

was restricted to the area between the eye and gape and a longitudinal line along the center of the throat. This specimen's dark head markings were more extensive than those on definitive-plumaged birds, and they were a duller, sooty, dark brown (see frontispiece).

Soft-part colors were relatively uniform across most specimens. The irides were brown or dark brown (all soft-part colors taken from tag data recorded at time of preparation) in nine specimens with adult characters, dark gray-brown in the three specimens with first-basic characters, and dark gray in the juvenile. Thus, iris color evidently changes from gray to dark brown as an individual ages. In all specimens, the maxilla was blackish-slate with a silvery-white tomium, the latter constricted at mid-bill in some individuals. Mandible coloration varied more. Most adults had a mostly silvery-white tomium with blackish-slate color on the gonys and base of the mandible (except the tomium). Approximately the distal half of the juvenile's bill was silvery-white, and the mouth interior was dark gray. The tarsus color of adult individuals was brownish-orange or ochre-orange; the juvenile's tarsi were dirty yellow with a gray tinge. The toes were dirty yellow, pale orange, or dull saffron yellow; the claws of the juvenile bird were gray.

Behavioral observations.—Our initial observations of *P. castaneus* were made by TVH and DFL at a swarm of *Eciton burchelli* army ants on 4 July 2001, when the first specimens were collected. Based on our observations, we were confident in labeling *P. castaneus* a professional army ant-follower (*sensu* Willis 1967). We never saw it foraging away from army ant swarms and observed it attending swarms of two army ant species: *Eciton burchelli* and *Labidus praedator*. For at least 12–15 min on 8 July, JAA observed a single individual of *P. castaneus* with a female Scale-backed Antbird (*Hylophylax poecilinota*) following a swarm of *L. praedator* ants that occupied less than 10 m^2 of the forest floor. The bird's behavior was similar to that of others observed following swarms of *E. burchelli*. Both the *P. castaneus* and the *H. poecilinota* individuals left the swarm for 3–4 min, only to return later. Also observed attending swarms of *L. praedator* (although independent of the above observation) were Allpahuayo Antbirds (*Percnostola arenarum*), a species previously unknown as an ant-follower (Isler et al. 2001, Zimmer and Isler 2003), and Bicolored Antbirds (*Gymnopithys leucaspis*). On four occasions on different days, we observed a single individual of *P. castaneus* quietly passing through the forest without foraging, suggesting movement between ant swarms or between an ant swarm and a nest (Willis 1981). In Table 2, we present the attendance of regular ant-following species observed at swarms at the Morona site.

Most often, *P. castaneus* was observed at or near the broad front of a moving ant column. Individuals tended to perch ≤0.5 m above ground and frequently dropped to the forest floor to investigate leaf litter or capture arthropods. Birds often were observed attending a swarm for 5 to 15 min at a time and then leaving the swarm (at least once while carrying a food item) for roughly equal periods of time. On at least one such occasion, a pair of *P. castaneus* was observed joining a family group of *G. leucaspis* moving between what appeared to be two column heads (about 30 m apart) of a single *E. burchelli* ant swarm. Willis (1981) reported similar behavior for *P. albifrons*. On another occasion, a single individual was seen moving around a standing hollow tree in which a swarm of *E. burchelli* had bivouacked the previous evening, but had not yet started its morning activity.

Most of the professional ant-following thamnophilids at the Morona site regularly made exaggerated tail "pounding" or "wagging" movements (terms following Zimmer and Isler 2003) while foraging at ant swarms, especially upon returning to a perch after pouncing on a prey item, or when agitated by the presence of an observer. *P. castaneus* was not observed regularly using any such tail movement. Only once or twice did we notice an individual pound its tail, usually after a pouncing attack on prey; the tail movement was made once and not repeated. By contrast, DFL noted that the *G. leucaspis* almost constantly wagged their tails laterally, although this contrasts with the published observations of others (e.g., Zimmer and Isler 2003). In addition, DFL observed both *P. albifrons* and the Reddish-winged Bare-eye (*Phlegopsis erythroptera*) regularly pounding their tails downward (also see Willis 1981, 1984; Zimmer and Isler 2003). We were unable to determine whether such tail movements are intended as a form of inter- or intraspecific "body language" among swarm attendants, as a sign of agitation, or as a form of flushing insect prey. Nevertheless, the relative lack of such tail-moving behavior in *P. castaneus* seems noteworthy. Willis (1968) reports that the monotypic genus *Skutchia* also lacks stereotypic tail-moving behavior, but other observers contest this (B. M. Whitney pers. comm.).

In our observations of ant-following birds at the Morona site (Table 2), we noted several occurrences of one ant-following species supplanting another near the leading edges of ant swarms and took this to represent a dominance hierarchy among the attendant species (see Willis 1967, 1981). From our observations, we concluded that the dominance hierarchy (from most to least dominant) was *Phlegopsis erythroptera*, *Pithys castaneus*, and *G. leucaspis*. Other swarm-attending antbirds, including *Pithys albifrons*, noticeably avoided the leading edge of the swarm when any of the other professional ant-followers were present. Our observations of the last species agree with those of Willis (1981), who also termed *P. albifrons* a subordinate ant swarm attendant. Since the dominance hierarchy suggested above has a positive correlation to overall body size, we suggest that size may be the ultimate cause (or, alternatively, a proximate cause—i.e., a source of maintenance) of the hierarchy (see Table 1).

Voice.—We recorded at least seven distinct vocalizations from *P. castaneus* (Fig. 2), including a mewed whistle that rises in frequency (Fig. 2A). This is a single note often given quietly, although occasionally it can be quite loud, and we suspect represents the species' "loudsong" (such as it is). To our knowledge, *P. albifrons* does not give a true loudsong (*sensu* Willis 1967, Isler et al. 1998, Isler and Whitney 2002, Zimmer and Isler 2003) as do most other thamnophilids. However, the species is known to produce a vocalization similar to that described above for *P. castaneus*: a rarely heard, weak, mewing whistled vocalization that falls in frequency and is suspected to serve as a song (Willis 1981, Isler and Whitney 2002; Fig. 2B). The whistled notes of the loudsong of *P. castaneus* appear to be punctuated by occasional quiet, chiming notes (Fig. 2C), perhaps an integral part of the loudsong. Song intervals can be as short as 2 sec but often are longer.

P. castaneus also produced two vocalizations when alarmed or when agitated by playback of what we believed was the species' song (see below). These notes of agitation were interspersed with sharp chattered "chit!" calls (Fig. 2D), similar to the "chip" calls described for *P. albifrons* by Willis (1981). Another vocalization given by agitated birds was a louder, higher-pitched "chirr," with the individual notes more distinct (Fig. 2E) than in the undisturbed chirr call (see below). Occasionally, the agitated chirr commenced with a chit note (Fig. 2F). While giving these vocal-

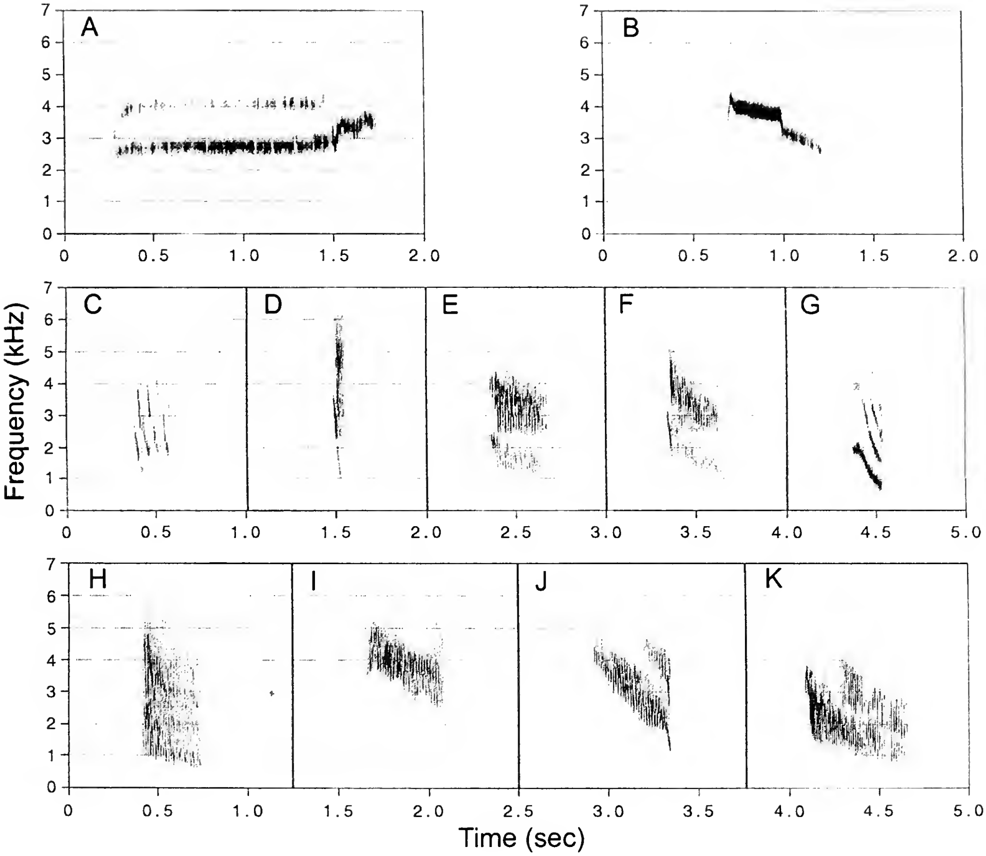

FIG. 2. Sound spectrograms of antbird vocalizations. Unless otherwise noted, all recordings were made by D. F. Lane at our Río Morona locality, Departmento Loreto, Peru, July 2001. (A) "Song" of *Pithys castaneus*. (B) "Song" of *Pithys albifrons* (T. A. Parker, III, and G. F. Budney, from Isler and Whitney 2002). (C) "Chime" of *Pithys castaneus*. (D) "Chit" of *Pithys castaneus*. (E) Agitated "Chirr" of *Pithys castaneus*. (F) "Chit-chirr" of *Pithys castaneus*. (G) "Mew" of *Pithys castaneus* (J. Alvarez A.). (H) "Chirr" of *Pithys castaneus*. (I) "Chirr" of *Pithys albifrons*. (J) "Chirr" of *Gymnopithys leucaspis*. (K) "Chirr" of *Phlegopsis erythroptera*.

izations of agitation, one male (sex confirmed by collection), was observed perched on a horizontal branch at the edge of a treefall gap about 2 m above the ground. This was the highest we ever observed the species to perch, and was likely an agitation response to playback of the song. On one occasion, a distinct, quiet, mewing "eaaah" call was given by two individuals while close to one another; we interpret this as some sort of contact call or "softsong" within the pair (Fig. 2G).

The most common vocalization was a call given by individuals while foraging at ant swarms. This was a deep chirr call (terms following Willis 1967, Zimmer and Isler 2003; Fig. 2H), similar to vocalizations given by most professional ant-following thamnophilids when attending ant swarms, and suspected to be a means of maintaining individual foraging space at the swarm (Willis 1967; M. L. Isler *in litt.*). When the chirr of *P. castaneus* was heard simultaneously with those of most of the other species of professional ant-followers at a swarm, it sounded generally louder, of lower overall frequency, and descended less obviously (see Fig. 2H–2K). Only the chirr call of *Phlegopsis erythroptera* (Fig. 2K) reaches a frequency as low as that of *Pithys castaneus*, but the former can be distinguished easily by a higher, more metallic introductory sound and a more sharply descending component. The chirr call of *Phlegopsis erythroptera* was louder than that of *Pithys castaneus* on occasion, but this appeared to be influenced by emotional state and was not always the case.

Playback experiments using recordings of the suspected song elicited varying reactions from individuals: some responded immediately, giving agitated calls and posing on exposed perches that were higher than typical perches (see above), while others approached silently to investigate. On two occasions, individuals approached only after 2–3 min of playback. Playback of chirr calls resulted in a quiet, curious approach at best.

DISCUSSION

Taxonomic status of the species.—Whereas the generic allocation of *Pithys castaneus* has been considered dubious, we believe that phenotypic characters such as the species' song-like vocalization, its bold chestnut plumage, black hood and white face, and its saffron-yellow legs all suggest a close relationship with *P. albifrons*. Furthermore, R. T. Brumfield and J. G. Tello (unpubl. data) have been building a molecular phylogeny of the Thamnophilidae, and have found *P. castaneus* and *P. albifrons* to be sister taxa.

Potential habitat specialization.—Based on our observations, we suspect that *P. castaneus* is restricted to *varillal* forests. We should note, however, that we observed and mist-netted *P. castaneus* individuals that had followed ant swarms from *varillal* into *varzea* forest immediately adjacent to our campsite, and twice we recorded individuals on richer, hilly *terra firme* forest within 300 m of typical *varillal* habitat. We never encountered Hairy-crested Antbird (*Rhegmatorhina melanosticta*) at the Morona site and wonder whether it may be replaced by the similarly sized *P. castaneus* (see Table 1) in the region or (more likely) habitat. We can find no evidence that *R. melanosticta* inhabits the region between the rios Santiago and Pastaza, but it is quite possible that this is due to poor sampling as it is to true absence. If *R. melanosticta* competitively excludes *P. castaneus* outside the Morona-Pastaza *varillal* forest, this may explain the restricted distribution of the latter species. Furthermore, if *varillal* forest habitat was not included in the searches conducted by Willis and the ANSP expedition along the Pastaza, their failure to encounter the species may be explained by the possible habitat specialization of *P. castaneus*.

Potential distribution of Pithys castaneus.—Landsat imagery, complemented with information from Instituto de Investigaciones de la Amazonía Peruana personnel and local people, shows what we interpret to be fairly large blocks of *varillal* forest embedded within a quadrangle formed by the Río Marañon to the south, the Río Morona to the east, the Río Mayuriaga to the north, and the Cordillera Campanquís to the west. Besides this area, *P. castaneus* populations are likely to occur in similar forest along the Río Pastaza in Loreto and probably into Ecuador. At present, we have no information about the existence of *varillal* forest at the latter sites. However, some indicator species of *varillal* forest have been found along the upper Río Pastaza in Ecuador (e.g., Pompadour Cotinga, *Xipholena punicea*, and Red-fan Parrot, *Deroptyus accipitrinus*; Ridgely and Greenfield 2001a), suggesting that the area probably supports *varillal* forest habitat. We suspect that once such forests along the upper Río Pastaza are located and surveyed, the mystery of the true position of the "Andoas" collecting locality finally will be unraveled.

Conservation.—The west bank of the Río Morona, including the areas of *varillal* forest where our work was conducted, are part of the recently created Zona Reservada Santiago Comaina, created in 1999. According to Peruvian legislation, its new status is temporary, but supposedly, it will be ranked as a definitive conservation unit in the future (National Park, National Reserve, National Sanctuary, or Communal Reserve). However, local leaders of the Federacion de Comunidades Indígenas del Rio Morona informed us that they strongly oppose the creation of a reserve and will fight to prevent this action.

A branch of the North-Peruvian oil pipeline that transports oil from the upper Río Pastaza passes through a large portion of *varillal* forest as it crosses the Río Mayuriaga on its way to the Río Marañon. At present, this has meant the destruction of only a 50-m-wide swath of forest along the pipeline. However, an oil spill could have drastic consequences for this rather delicate habitat, particularly with its flat terrain and poor drainage. Furthermore, the pipeline itself could represent a potential dispersal barrier for *P. castaneus*. It is also worth mentioning that there are several plans to connect Ecuador's Amazonian road network to the Río Marañón. Anecdotal evidence suggests that many bird species of interior forest understory are averse to crossing large openings or other similar breaks, such as rivers or roads (Zimmer and Isler 2003). Thus, gaps such as those associated with roads and pipelines may pose barriers to gene flow in populations of these understory species.

Population estimate.—During our stay we surveyed about 8 km^2 of white-sand forests and encountered between six and eight different army ant swarms of *E. burchelli* and two of *L. praedator*. Based on our extrapolations, we estimate the number of *P. castaneus* to be between 18 and 26 individuals in the area we surveyed. If we consider the immediate area (the Morona-Santiago interfluvium) covered with *varillal,* then the population estimate of *P. castaneus* would be ~1,300–2,500 individuals. Prior to our rediscovery of *P. castaneus*, the species was considered to be rare, with a very restricted global distribution, and probably threatened (Bibby 1992, Stattersfield and Capper 2000). Considering the population estimates and the potential threats presented here, we recommend changing the species' status from Data Deficient to Vulnerable, according to the ranking criteria presented in Stattersfield and Capper (2000). If a road or any other invasive construction project threatens the white-sand forests between the ríos Morona and Santiago, then the species' status should be upgraded to a category of higher risk.

Since our rediscovery of *P. castaneus* in July 2001, and our discovery of the two Treneman specimens in MUSM, we have been informed of two subsequent observations of *P. castaneus* by colleagues who visited our Morona site. Observers visited the site 22–24 June 2002 and 24 May 2003 (M. Levy, J. Nilsson, M. Sokol, and B. Walker pers. comm.). Both parties saw the species, but the 2002 observation was of multiple individuals and the observers regarded the species as "one of the most common birds" at the site. During the 2003 visit, however, only one individual was observed, possibly because swarms of army ants were not easily encountered then (an artifact of the season?).

ACKNOWLEDGMENTS

We thank J. P. O'Neill as the initiator and organizer of the 2001 expedition. Funding for the 2001 expedition was received from the Coypu Foundation and a donation from the late R. B. Wallace. Additional funding was provided to JAA by a Fulbright Scholarship. Permits for fieldwork were granted by INRENA, and we particularly appreciate the efforts of M. Prieto C. and R. Acero V. of that institution. D. Huachaca, M. Sánchez S., A. Urbay T., M. Pizango, M. Tenazoa, H. Pizango, F. Salazar, and R. Sandoval all provided logistical support in the field. M. L. and P. R. Isler graciously allowed us access to their data and recording collections, and freely provided the fine maps and sonograms for our figures. M. Levy, J. Nilsson, M. Sokol, and B. Walker all related information from their visits to the Morona site. T. Mark provided us with his Andoas manuscript, and he and J. W. Fitzpatrick provided information and photos of the holotype at the Paris Museum. L. B. McQueen produced the illustration that allowed us to recognize *Pithys castaneus* while in the field. T. S. Schulenberg provided us with rare reprints and data collected on Peruvian antbirds. I. Franke J. kindly allowed us access to the ornithological collection in her care at MUSM, and assisted us in trying to find more details of the two "mystery" *Pithys castaneus* specimens there. This manuscript benefited from comments by M. L. and P. R. Isler, J. V. Remsen, Jr., T. S. Schulenberg, B. Walker, B. M. Whitney, K. J. Zimmer, and two anonymous reviewers.

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The Wilson Journal of Ornithology 118(1):23–35, 2006

NESTING ECOLOGY OF LESSER PRAIRIE-CHICKENS IN SAND SAGEBRUSH PRAIRIE OF SOUTHWESTERN KANSAS

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ABSTRACT.—Despite the fact that the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) is a species of conservation concern, little is known about its nesting ecology, particularly in sand sagebrush (*Artemisia filifolia*) habitats. To find and monitor nests, we captured and equipped 227 female Lesser Prairie-Chickens with transmitters (87 yearlings, 117 adults, and 23 of unknown age) from 1997 to 2002 in southwestern Kansas. Apparent nest success was similar for yearlings (31%, $n = 74$) and adults (27%, $n = 97$) but differed marginally ($P = 0.090$) between first nests (29%) and renests (14%). An estimated 31% of females that were unsuccessful in their first nesting attempt initiated a second nest. The probability that a female would initiate a second nest after failure of the initial attempt was negatively influenced by the day of incubation on which the initial attempt failed. Over 95% of all nests were initiated and completed between 5 May and 2 July. The primary cause of nest failure was predation by coyotes (*Canis latrans*) and gopher snakes (*Pituophis melanoleucus*). Mean clutch size, egg fertility, hatching success, nesting and renesting frequency, and incidence of interspecific parasitism were all similar across years and between yearlings and adults. Distances between nest sites were used as an index to nest-site fidelity between first nests and renests and for across-year nesting attempts. Mean distances between first nests and renests were similar for yearlings (1,071 m) and adults (1,182 m). Mean distance between nests constructed by the same female in subsequent years (918 m) did not differ between age classes or success of the first year's nest. Most females (80%) nested closer to a lek other than the lek where they were captured.
Received 24 January 2005, accepted 21 September 2005.

Range-wide, Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) have declined by an estimated 97% since the 1800s (Crawford 1980, Taylor and Guthery 1980). In Kansas, Lesser Prairie-Chickens are most abundant in the western part of the state—south of the Arkansas River in mixed and shortgrass prairie dominated by sand sagebrush (*Artemisia filifolia*). They also occur in mixed grass prairie north of the Arkansas River, but this habitat is generally devoid of sand sagebrush. Lesser Prairie-Chickens currently occupy 31 of 39 counties believed to compose their historical distribution in Kansas, but counts of leks and individual birds suggest that Lesser Prairie-Chickens have experienced significant declines since 1964 (Jensen et al. 2000).

The mechanisms responsible for Lesser Prairie-Chicken population declines have not been identified; however, aspects of nesting ecology could be influential (Peterson and Silvy 1996, Wisdom and Mills 1997). Thus, identifying age-specific variation in nesting variables is important to understanding a species' demography or life-history strategy (Patten et al. 2005). Most research on Lesser Prairie-Chicken nesting ecology has been conducted in sand shinnery oak (*Quercus havardii*) habitats in New Mexico and Texas (Davis et al. 1979, Haukos and Broda 1989, Riley et al. 1992). The objectives of our study were to provide baseline information on age-specific variation in nesting ecology, record fidelity to previous nest sites (within-year renests and across-year attempts), and document nest-site locations relative to leks of Lesser Prairie-Chickens in sand sagebrush prairie of southwestern Kansas. We examined annual variation and the effects of age on reproductive parameters and nest-site placement.

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METHODS

Study area.—From 1997 to 2002, we studied Lesser Prairie-Chickens inhabiting sand sagebrush habitat south of the Arkansas River in Finney County, Kansas (37° 52′ N, 100° 59′ W). We initiated field work on a 7,700-ha area in 1997 and on a nearby 5,600-ha area in 2000; we continued work on both areas through summer 2002. Vegetation was similar in both areas; sand sagebrush was the most conspicuous vegetation present and was interspersed with grasses, including little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Stipa comata*), sand lovegrass (*Eragrostis trichodes*), sixweeks fescue (*Vulpia octoflora*), blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), sideoats grama (*B. curtipendula*), and western wheatgrass (*Agropyron smithii*). The most common forb species were Russian thistle (*Salsola kali*), western ragweed (*Ambrosia psilostachya*), sand lily (*Leucocrinum montanum*), and common sunflower (*Helianthus annuus*). Each study area was bounded almost entirely by center-pivot irrigated cropland and grazed seasonally by livestock. Annual precipitation averaged 50 cm (U.S. Department of Commerce 2003) and ranged from 42 cm (2000) to 59 cm (1997) during our study.

Locating and monitoring nests.—Using walk-in funnel traps, we captured female Lesser Prairie-Chickens on leks from mid-March through mid-April (Haukos et al. 1990). Except in 1997 (when age was not determined), we classified captured birds as yearlings (~10 months of age) or adults (≥21 months of age) by examining the primaries (Copelin 1963). We equipped birds with 11-g necklace-style transmitters (life expectancy = 6–12 months; models from AVM Instrument Company, Colfax, California; Advanced Telemetry Systems, Isanti, Minnesota; and Holohil Systems, Carp, Ontario) and released them on-site immediately after capture. Each day, we determined locations of transmitter-equipped birds by triangulating bearings collected from a truck-mounted, null-peak telemetry system. Bird locations were determined until transmitter failure, emigration from the primary study areas, or bird death. When birds emigrated from our study area, we re-located them by extensive ground searches or from fixed-wing aircraft. We monitored females that moved off our study area two to three times per week throughout the nesting season.

Using a hand-held antenna, we found nests by approaching transmitter-equipped females when their locations had remained unchanged ≥3 consecutive days. If the female was incubating, she was flushed so the eggs could be counted and the clutch examined for interspecific parasitism (Hagen et al. 2002). We marked nest locations with flags (1997) or transmitters (1998–1999) at a distance of 5 m from the nest bowl (Jamison 2000), or we recorded locations with a global positioning system (2000–2002). Nest sites were not visited again until the female departed the site with a brood or until the nest was depredated or abandoned. This technique allowed us to estimate apparent nest success only. Because we did not determine nest status throughout incubation, we did not estimate daily survival of eggs or nests according to the Mayfield method (Mayfield 1975).

After the departure of each nesting female, we classified nest fate as successful (produced at least one chick), unsuccessful, or abandoned. Beginning in 2000, we opened unhatched eggs to determine whether embryos had developed. If the nest was depredated, we systematically searched the area within a 10-m radius for tracks, scat, or eggshell fragments to help determine the predator's identity (Sargeant et al. 1998).

Statistical analyses.—We recorded clutch size and estimated the start of incubation for yearling and adult nests. We defined the start of incubation as the first day on which we detected no changes in the female's telemetry locations—typically, 3–5 days before a nest was located. We estimated the initiation date of each nest by backdating from the start of incubation by 1 day for each egg in the clutch (Coats 1955). We also calculated apparent nest success (the proportion of all known nests producing at least one chick × 100), hatching success, egg fertility, percentage of females attempting a nest, percentage of females renesting, and the incidence of interspecific parasitism—separately for yearlings and adults. We defined hatching success as the number of eggs hatched divided by initial clutch size (Westemeier et al. 1998b). We defined percent fertility as the number of eggs hatching or containing a developed embryo divided by the total number of eggs in the nest bowl at the time of hatching. We estimated incubation length as the time (days) between the start of incubation and the date when a female left the nest with a brood (as determined from telemetry locations). We estimated nesting frequency as the percentage of females that attempted a nest. Females that did not attempt a nest and died before 31 May were excluded from our estimate of nesting frequency. Because we documented some first nesting attempts after 31 May, it was uncertain whether birds dying prior to this date would have subsequently attempted a nest. Interspecific parasitism was reported as the percentage of nests containing eggs of both Lesser Prairie-Chickens and other bird species. Interspecific nest parasitism was previously described for the 1997 to 1999 field seasons (Hagen et al. 2002); here, we summarize all records of parasitism from 1997 to 2002. The percentage of females attempting to renest was estimated as the percentage of females known to have incubated and lost a first clutch and that subsequently incubated a second. Because of some small expected cell counts, we used a Fisher's exact test for all comparisons (Agresti 1996). In addition, we used two-tailed *t*-tests for unequal variances (Zar 1999) to compare clutch size, incubation date, hatch date, and incubation length between yearlings and adults.

We used logistic regression to assess the relationship between the likelihood of renesting and (1) age class, (2) clutch size of the initial nest attempt, and (3) day into incubation when the initial attempt failed. We excluded data from 1997 because we did not identify age class of birds that year. Initially, we fit seven *a priori* models to data associated with 59 failed first nest attempts recorded from 1998 to 2002. We considered all four additive models and main effect models for each of the three independent terms. We used the minimization of Akaike's Information Criterion for small sample sizes (AIC_c) to rank the models (Burnham and Anderson 1998). All models where $\Delta AIC_c \leq 2$ were considered to be competing models (Burnham and Anderson 1998). Because age class was not included in any of the competing models (all $\Delta AIC_c > 2$), we excluded this variable and developed models using an expanded data set ($n = 69$) that included failed first nest attempts recorded from 1997 to 2002. We used the same model procedures previously described to fit three of our *a priori* models that included the main effects (1) clutch size and (2) day of incubation on which the initial attempt failed.

We calculated distances between first nests and renests, nesting attempts in multiple years, and distances from nest sites to the lek of capture and the nearest lek. We used analysis of variance (ANOVA) to determine whether year or age class influenced the distance between an initial nest site and the renest location and the affinity of nesting females to lek sites (capture lek and nearest lek). We also used ANOVA to determine whether age class or success of the first-year nest affected distance between nest sites in subsequent years. For these analyses, we excluded all data from 1997 because we did not identify age class that year; however, we included pooled age-class data from 1997 in the data tables to provide an overview of nesting parameters for the duration of our study. We interpreted simple effects with two-sample *t*-tests when significant interactions were found (Zar 1999). We considered all differences significant when $P < 0.05$ and marginally significant when $0.05 < P < 0.10$. We report parameter estimates and means as ± SE (or SD as noted).

RESULTS

Nesting ecology.—We captured 227 female Lesser Prairie-Chickens and fitted them with transmitters (87 yearlings, 117 adults, and 23 of unknown age). We found 209 nests (77 yearling, 103 adult, and 29 unknown-age). The percentage of females initiating a nest was similar ($P = 0.50$) for yearlings (94%) and adults (92%; Table 1). We determined fate for 196 of 209 (94%) nests; apparent nest success was 26 ± 3% (51 of 196). The remaining nests were either abandoned (2%, $n = 5$) or success could not be determined from evidence remaining at the nest site (4%, $n = 8$). Nest success did not differ across years ($\chi^2 = 6.95$, df $= 5$, $P = 0.22$) or between age classes for first nests ($P = 0.60$) or renests ($P = 0.82$; Table 1). An estimated 31% of all females that were unsuccessful in their first nesting attempt initiated a second nest, and this percentage did not differ ($P = 0.85$) between yearlings and

TABLE 1. Lesser Prairie-Chicken nesting statistics (mean ± SE), by nesting attempt and age, compiled over a 6-year period in the sand sagebrush prairie of southwestern Kansas, 1997–2002.

Attempt/Variable	*n*	Yearling	*n*	Adult	*P*	*n*	All females[a]
First nest							
Nest success (%)	60	35 ± 5	78	31 ± 5	0.60	157	29 ± 4
Clutch size	61	11.8 ± 0.2	81	12.3 ± 0.2	0.079	161	12.0 ± 0.1
Start of incubation (Julian date)	57	127.4 ± 0.9	76	127.3 ± 0.9	0.94	151	128.5 ± 0.7
Hatch date (Julian date)	20	156.7 ± 2.0	24	151.4 ± 1.6	0.044	45	153.8 ± 1.3
Second nest							
Nest success (%)	13	15 ± 10	16	13 ± 8	0.82	35	14 ± 6
Clutch size	11	8.2 ± 0.6	14	7.3 ± 0.6	0.30	29	7.6 ± 0.4
Start of incubation (Julian date)	13	153.9 ± 2.2	15	152.9 ± 1.9	0.73	34	153.3 ± 1.3
Hatch date (Julian date)	2	175.5 ± 1.5	2	167.0 ± 3.0	0.13	5	175.0 ± 4.3
Pooled							
Nest success (%)	74	31 ± 5	97	27 ± 5	0.54	196	26 ± 3
Incubation length (days)	21	27.3 ± 0.6	20	26.3 ± 0.6	0.25	43	26.7 ± 0.4
% eggs hatching	235	75 ± 3	323	72 ± 3	0.50	570	74 ± 2
% eggs fertile	87	94 ± 3	223	95 ± 2	0.90	311	94 ± 1
% females nesting[b]	70	94 ± 3	82	92 ± 3	0.50	176	92 ± 2
% females attempting a renest	39[c]	33 ± 8	54[c]	31 ± 6	0.85	112[c]	31 ± 4
% nests parasitized[d]	77	4 ± 2	103	3 ± 2	0.72	209	3 ± 1

[a] Includes females of unknown age.

[b] Females that attempted a nest; females that did not attempt a nest and died before 31 May were excluded.

[c] *n* = number of failed first nests.

[d] Nests were parasitized by either Ring-necked Pheasants or Northern Bobwhites.

adults (Table 1). However, success of renests (14%) was marginally less than success of initial nests (29%; $\chi^2 = 3.31$, df = 1, $P = 0.090$). No females were known to have initiated a third nest in the same year. Mean hatch date (all years combined) was 1 June for first nesting attempts and 22 June for renests (Fig. 1), with a mean incubation length of 26.7 days (Table 1). More than 95% of all nests were initiated and completed between 5 May and 2 July (Fig. 1).

Mean clutch size did not differ between yearlings and adults for either first nesting or renesting attempts (Table 1). Mean clutch size was 7.6 ± 0.4 eggs for renests, significantly less ($t_{188} = 11.77$, $P < 0.001$) than the mean clutch size (12.0 ± 0.1 eggs) of first nests. Overall hatching success was 74 ± 2% and did not differ between yearlings and adults. Likewise, egg fertility was similar between the two age classes, with 94 ± 1% of all eggs containing a developed embryo (Table 1).

Six of 209 (3%) Lesser Prairie-Chicken nests were parasitized by other bird species. Four of the six nests contained Lesser Prairie-Chicken and Ring-necked Pheasant (*Phasianus colchicus*) eggs, and eggs of both species hatched in two of these nests. One nest was parasitized by a Northern Bobwhite (*Colinus virginianus*; 10 prairie-chicken eggs and 1 quail egg), and the remaining nest was parasitized by both Ring-necked Pheasant and Northern Bobwhite (3 prairie-chicken eggs, 1 pheasant egg, and 1 quail egg). Both of these latter nests were depredated before hatching.

Nest predators.—Most (>80%) known predation events occurred >3 days after our initial nest visit (mean = 10.2 days ± 6.9 SD). We assigned predator species to 112 of 161 (70%) unsuccessful Lesser Prairie-Chicken nests. Coyotes (*Canis latrans*) depredated the majority (64%) of the nests and were the primary cause of nest predation during most years (Table 2). Snakes were responsible for the loss of 31% and 42% of the unsuccessful Lesser Prairie-Chicken nests in 2001 and 2002, respectively. Most of the snake predation was probably by Gopher snakes (*Pituophis melanoleucus*) because they were the most observed snake species on our study areas. Other causes of nest loss included predation by ground squirrels (*Spermophilus* spp.) and trampling by cattle (Table 2).

Renesting probability.—The probability of a Lesser Prairie-Chicken renesting was influenced by both clutch size and the day of incubation on which the initial attempt failed. An additive model including both terms was the highest-ranking ($\Delta AIC_c = 0.00$; $AIC_c = 80.90$), but the model including only date of failure also had considerable support ($\Delta AIC_c = 1.48$). The model including only clutch size was not supported ($\Delta AIC_c = 15.24$). Females incubating initial nests later into incubation tended to have a lower probability of renesting ($ß_{date} = -0.18$, 95% CI = −0.28 to −0.08; Fig. 2). Females laying a larger clutch in the initial nest attempt tended to be more likely to renest ($ß_{clutch} = 0.31$); however, the magnitude of this effect was not clear because the confidence interval overlapped zero (95% CI = −0.01 to 0.63). The odds of a female attempting to renest decreased by 16.2% with each day into incubation of the initial attempt and increased 20.2% with each one-egg increase in clutch size (Fig. 2).

Nest-site location.—Between 1997 and 2002, we found 28 renests (Table 3). Distance between first nests and renests (1,271 m) was not influenced by age class ($F_{1,23} = 1.69$, $P = 0.21$) or year ($F_{4,23} = 1.65$, $P = 0.21$); there was no interaction effect ($F_{2,23} = 1.82$, $P = 0.19$; 1998–2002 data). Similarly, the distance between nests initiated by the same female in subsequent years (mean = 918 m, $n = 15$; Table 3) was not influenced by age class ($F_{1,14} = 0.16$, $P = 0.70$) or success of the first-year nest ($F_{1,14} = 0.05$, $P = 0.82$); there was no interaction effect ($F_{1,14} = 0.00$, $P = 0.98$).

The distance from a nest to the nearest lek (mean = 691 m, $n = 194$; Table 4) was not influenced by year ($F_{4,164} = 1.11$, $P = 0.36$) or age class ($F_{1,164} = 0.00$, $P = 0.99$), nor was there an interaction effect ($F_{4,164} = 1.41$, $P = 0.23$; 1998–2002 data). Of 184 nests, 147 (80%) were located closer to a lek other than the lek where the female was last captured. Ten nests (5%) were located >10 km from the lek at which the incubating female was captured (median = 20.6 km, range = 10.6–56.5 km). The female nesting 56.5 km from her lek of capture was successful in her nesting attempt. The distance from nest site to the lek where the female was captured (mean = 3,082 m, $n = 184$; Table 4) was not influenced by age class ($F_{1,158} = 0.12$, $P = 0.73$) or year

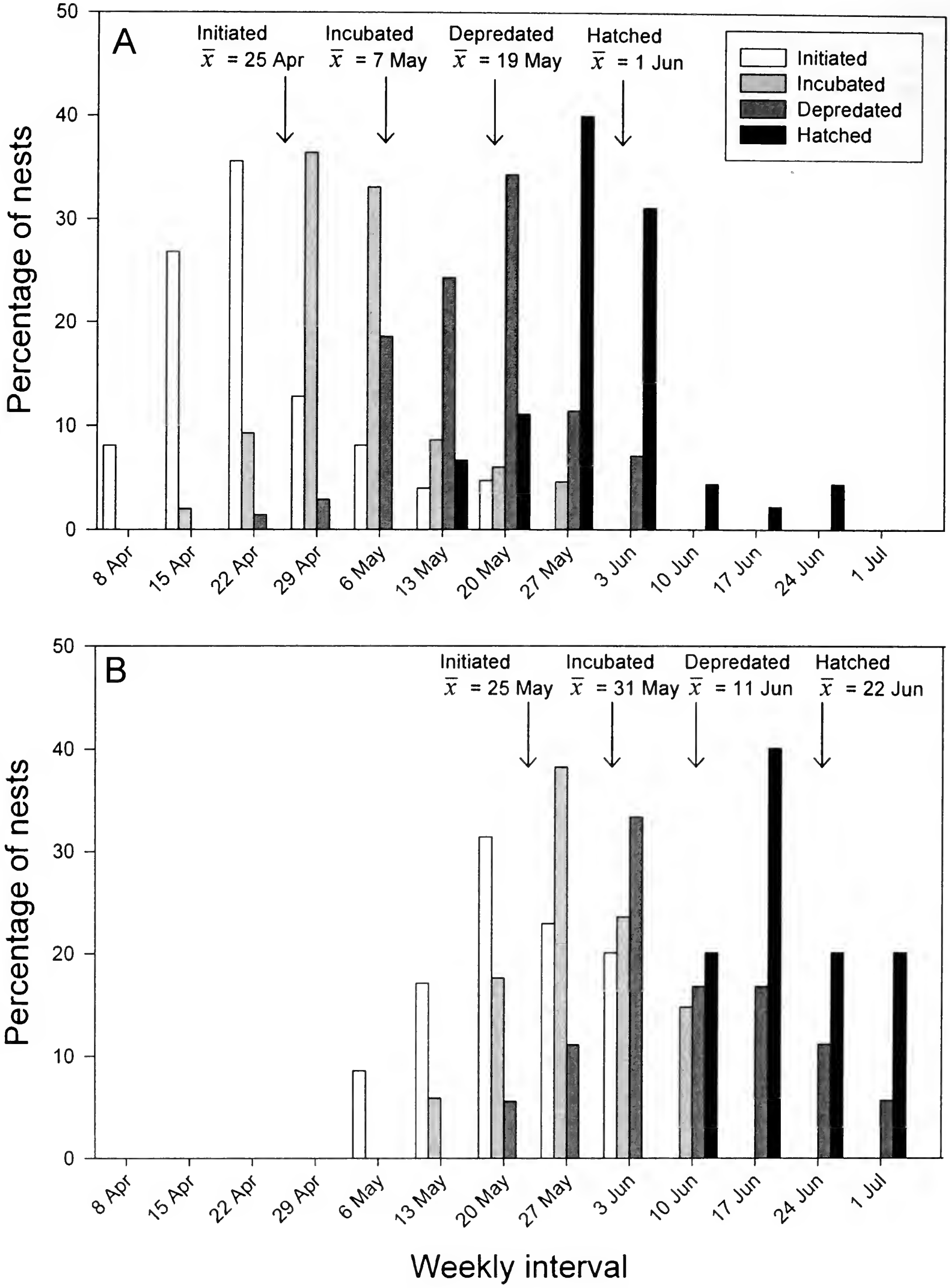

FIG. 1. Percentage of Lesser Prairie-Chicken first nests (A) and renests (B) in southwestern Kansas that were initiated, incubated, depredated, and hatched, by weekly intervals, 1997–2002. Mean dates for each variable are listed at the top of each figure.

TABLE 2. Probable causes of predation of Lesser Prairie-Chicken nests in the sand sagebrush prairie of southwestern Kansas, 1997–2002.

	Depredation (%)						
Predator	1997 (n = 24)	1998 (n = 12)	1999 (n = 20)	2000 (n = 44)	2001 (n = 36)	2002 (n = 26)	Total[a] (n = 161)
Coyote	71	100	70	34	22	27	45
Ground squirrel[b]	4	0	0	11	0	0	4
Snake[c]	13	0	5	11	31	42	19
Cattle	0	0	5	2	3	0	2
Unknown	13	0	20	41	45	31	30

[a] Percentage of all nests destroyed by each predator.

[b] We did not differentiate between thirteen-lined ground squirrels and spotted ground squirrels.

[c] Gopher snakes appeared to be the most abundant snake species.

($F_{4,158}$ = 1.25 P = 0.29), and there was no interaction effect ($F_{4,158}$ = 1.33, P = 0.26; 1998–2002 data).

DISCUSSION

Although rainfall during the primary 4-month nesting period (April through July) varied substantially during the 6 years of our study (range = 22.3–38.3 cm), we documented little annual variation in Lesser Prairie-Chicken nesting activity. Our ability to detect annual variation, however, may have been hindered by relatively small sample sizes within years, especially in the early years of the

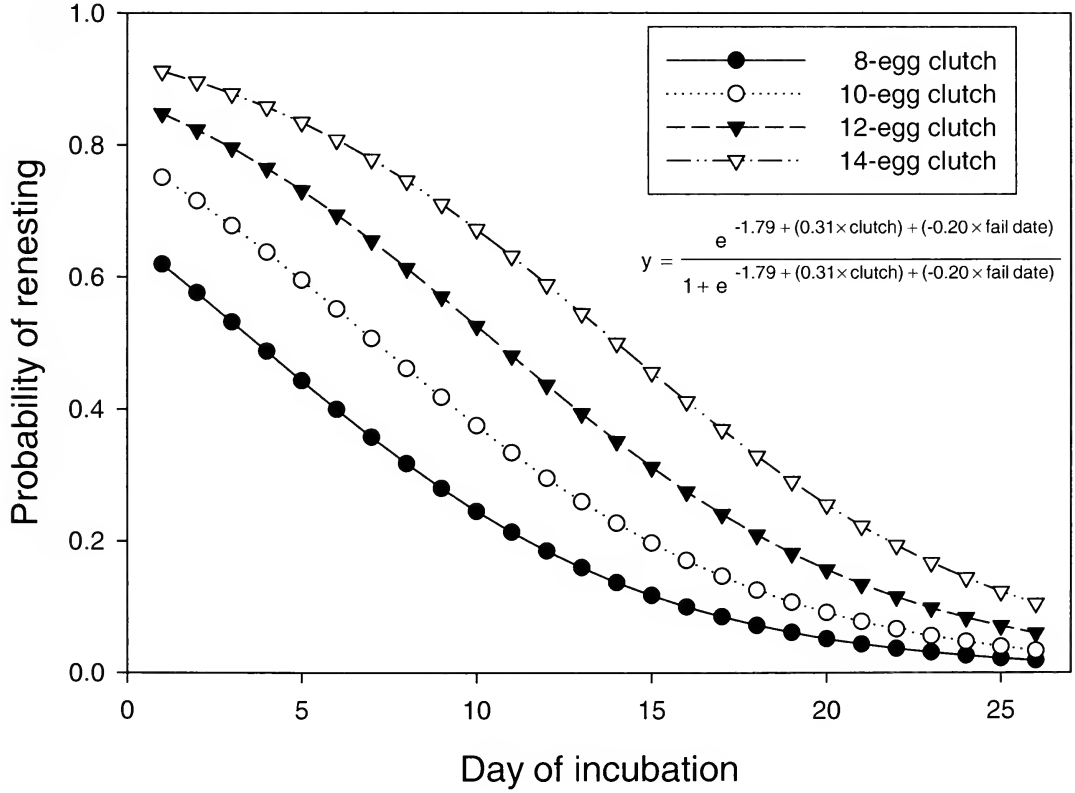

FIG. 2. Probability of Lesser Prairie-Chickens initiating renests after failure of the initial nest attempt in southwestern Kansas, 1997–2002. Probabilities are plotted for various clutch sizes (8, 10, 12, 14) and the day of incubation when the initial nest attempt failed.

TABLE 3. Evidence of nest-site fidelity as shown by mean distances (m) between nests for Lesser Prairie-Chickens in southwestern Kansas, 1997–2002. Within- and across-year distances are presented by age class and nest fate.

Category	Within-year[a]			Across years[b,c]		
	n	Distance	SE	*n*	Distance	SE
Age class						
Yearling	11	1,071	327	6	1,170	599
Adult	13	1,182	263	9	750	365
Nest fate[d]						
Successful	—	—	—	6	712	438
Unsuccessful	—	—	—	9	1,055	453
Total[e]	28	1,271	218	15	918	316

[a] Distance between the first nest and the renest.

[b] For two females that initiated ≥1 nest within a year, the mean coordinates of those nests were used to calculate the distance to the nest site in subsequent years.

[c] Nests for one female were located in non-consecutive years; all other nests were located in consecutive years.

[d] Nest fate refers to fate of first nests.

[e] Age of four females was undetermined.

study. Additionally, we observed little age-specific variation—except that yearlings had slightly smaller clutches and marginally later hatch dates for first nest attempts than did adults.

For all known nests, initiation began in early May; peak hatching was 1 June for first nests and 22 June for renests (Fig. 1). Similar dates of nest initiation (mid-April through late May) and hatching (late May through mid-June) have been reported from studies throughout the species' range (Giesen 1998, Patten et al. 2005). Mean incubation length was 26.7 days (this study). Because nest attentiveness of grouse increases throughout the laying period (Giesen and Braun 1979), we may have overestimated incubation length by misidentifying the start of incubation. However, the time required to hatch Lesser Prairie-Chicken eggs in an incubator (24–26 days; Coats 1955, Sutton 1968) was only slightly less than our estimate for eggs incubated by wild birds.

The success of all nests averaged 26% in our study, substantially less than estimates from New Mexico (42%) and Oklahoma (40%; Patten et al. 2005), but similar to the 28% reported by Giesen (1998) for 10 studies

TABLE 4. Distances (m) between Lesser Prairie-Chicken nest sites and leks in southwestern Kansas, 1997–2002.

Category	Nest site to lek of capture			Nest site to nearest lek		
	n	Median	Mean ± SE	*n*	Median	Mean ± SE
Year						
1997	25	1,528	1,647 ± 226	26	556	557 ± 52
1998	14	1,134	1,727 ± 529	14	577	546 ± 71
1999	24	2,357	2,317 ± 332	25	726	701 ± 55
2000	56	1,282	2,874 ± 1,006	56	675	742 ± 53
2001	37	1,396	3,241 ± 983	41	727	740 ± 54
2002	28	2,333	5,901 ± 1,366	32	631	703 ± 65
Age						
Yearling	68	1,893	3,580 ± 853	68	633	702 ± 48
Adult	91	1,258	3,104 ± 591	97	675	718 ± 32
Total	184[a]	1,427	3,082 ± 432	194[b]	632	691 ± 25

[a] Includes 25 nests of females of unknown age.

[b] Includes 29 nests of females of unknown age.

conducted throughout the range of the Lesser Prairie-Chicken. Giesen (1998) suggested that nest success from those 10 studies was negatively biased due to observer disturbance at nest sites. Negative bias in our study was likely only slight because females were flushed from their nests only once. Westemeier et al. (1998a) reported that flushing incubating Greater Prairie-Chickens (*T. cupido*) once did not result in reduced nest success. Also, the number of days between our initial nest visits and predation events averaged >10 days. In addition, only 2% of the nests in our study were abandoned—a much smaller percentage than the 25% reported by Riley et al. (1992) for Lesser Prairie-Chickens in New Mexico. Further, one of five nests abandoned during our study was abandoned 9 days after the researcher's visit, indicating that it probably was not due to human disturbance.

The percentage of females initiating a second nest during our study (31%) was between previous estimates for Lesser Prairie-Chickens in New Mexico (15%) and Oklahoma (79%; Patten et al. 2005), and it was less than the 83% reported for Greater Prairie-Chickens (Svedarsky 1988) and the 67% estimated for Sharp-tailed Grouse (*T. phasianellus*; Roersma 2001). The percentage of Greater Sage-Grouse (*Centrocercus urophasianus*) initiating a renest was highly variable (5 to 87%) throughout their range (Schroeder et al. 1999), and most estimates were less than what we observed for Lesser Prairie-Chickens. Our models indicated that the low probability of Lesser Prairie-Chickens renesting in southwestern Kansas was influenced by the length of incubation before their clutches were depredated (>50% of unsuccessful initial clutches were incubated >12 days prior to predation). Similarly, Schroeder (1997) reported that Greater Sage-Grouse in Washington whose initial nests failed late in incubation were less likely to renest than those whose nests failed earlier in incubation. Clutch size of the initial nesting attempt was also somewhat associated with renesting probability in our study; however, the magnitude of this effect was unclear. The positive relationship that we observed may have been due to increased fitness associated with females laying larger clutches or the possibility that we misclassified some renests as initial nest attempts. We speculate that the latter was not a common occurrence during our study, but our methods did not allow us to locate nests that were depredated prior to the onset of incubation.

Few prairie grouse researchers have reported nest success separately for first nest attempts and subsequent renestings. Bergerud and Gratson (1988) hypothesized that predation of grouse nests was density-dependent and that renests would be more successful than first nest attempts due to lower nest densities. They also believed that nest success should improve as new vegetative cover appears throughout the nesting season. Success of first and second nesting attempts of Lesser Prairie-Chickens in Kansas, however, does not support Bergerud and Gratson's (1988) hypotheses, as first nest attempts were marginally more successful than renestings. Likewise, Greater Prairie-Chicken nests initiated in Kansas prior to 30 April (presumably first attempts) were more successful than nests initiated after 1 May (presumably renests; Robel 1970). Initial nesting attempts for Attwater's Greater Prairie-Chicken (*T. c. attwateri*) also were more successful than renests in 4 of 5 years (Lutz et al. 1994). Similar nest success for first attempts and subsequent renestings has been reported for Greater Prairie-Chickens in Colorado (Schroeder and Braun 1992) and Greater Sage-Grouse in Washington (Schroeder 1997) and Alberta, Canada (Aldridge and Brigham 2001). The only support for Bergerud and Gratson's (1988) hypothesis comes from studies on Sharp-tailed Grouse in Minnesota and North Dakota, where success was higher for second attempts than first attempts (Christenson 1970, Schiller 1973). In our study, Lesser Prairie-Chicken nests initiated after 15 May were less successful (11.9%, $n = 42$) than earlier nests (31.5%, $n = 143$), regardless of nesting attempt. We speculate that nests initiated after 15 May were less successful due to an increase in predator efficiency later in the nesting season, corresponding to changes in the structure and composition of vegetation. Cattle grazing began on our study area around 15 May, and, after that date, grass cover and visual obstruction decreased substantially (JCP unpubl. data). Grazing coupled with normal drought conditions during the summer months in southwestern Kansas may result in declining habitat quality, and, therefore, the poor success of renesting Lesser Prairie-Chickens. Land management practices that maintain taller and denser vegetation structure later into the nesting season may promote the overall nesting success of Lesser Prairie-Chickens.

Clutch size in Kansas averaged 11.3 eggs in 191 completed clutches—greater than that reported in New Mexico (8.7) and Oklahoma (10.8; Patten et al. 2005) or in 60 completed clutches located in other states occupied by Lesser Prairie-Chickens (10.4; Giesen 1998). Our study is the first to document substantially different mean clutch sizes for first nests (12.0 eggs) and renests (7.6 eggs). Merchant (1982) reported mean clutch size for initial and second nesting attempts, but his estimates were similar for both (9.8 and 10.7 eggs, respectively). In our study, the percentage of eggs containing a developed embryo was 94% and hatching success was 74%. Egg fertility has not been reported previously for the Lesser Prairie-Chicken, but hatching success of eggs was estimated at >90% across three studies (see Giesen 1998). The lower hatching success observed in our study reflects partial nest losses that occurred in 32 of 48 (67%) successful nests.

Identifying nest predators from nest remains is difficult because patterns of egg breakage overlap among, and even within, predator species (Larivière 1999). Uncertainties were reduced on our study area, however, because coyotes and gopher snakes were the only common species capable of preying on Lesser Prairie-Chicken nests. Studies in New Mexico and Texas revealed that Chihuahuan Ravens (*Corvus cryptoleucus*), badgers (*Taxidea taxus*), striped skunks (*Mephitis mephitis*), and ground squirrels were the primary predators of Lesser Prairie-Chicken nests (Davis et al. 1979, Haukos and Broda 1989, Riley et al. 1992). However, few corvids, badgers, or striped skunks were observed on our study area, and, although ground squirrels were abundant (estimated from casual roadside observations), they were identified as important nest predators during only 1 year (2000).

Davis et al. (1979) documented snakes preying on Lesser Prairie-Chicken nests in New Mexico. We found little evidence for snake predation of nests during the early years of our study (Jamison 2000), but snake abundance appeared to increase (estimated from casual roadside observations), as did nest predation by snakes, in the later years (Pitman 2003). Snakes may have been responsible for most partial-nest depredations because of the lack of eggshell fragments at partly depredated nests. Also, three incubating Lesser Prairie-Chickens were likely killed by snakes because their intact carcasses were found with a thin film of mucus covering the heads. In each case, it appeared as if a snake had tried to swallow the bird.

Interspecific nest parasitism has been reported for Greater Prairie-Chickens and Sharp-tailed Grouse (Leach 1994, Westemeier et al. 1998b), but had not been reported for Lesser Prairie-Chickens before our work in Kansas (Hagen et al. 2002). Only 6 of 209 (3%) nests were parasitized by Ring-necked Pheasants and/or Northern Bobwhites, and 2 of the 6 (33%) nests produced Lesser Prairie-Chicken chicks. Hatching success of eggs in these two nests was 72%, similar to the 74% estimated for 46 unparasitized nests (Hagen et al. 2002). Our study provided no evidence that nest parasitism negatively affected nest success or hatchability of Lesser Prairie-Chickens.

Bergerud and Gratson (1988) hypothesized that successful female grouse would nest in the same area in the subsequent breeding season. In southwestern Kansas, female Lesser Prairie-Chickens nested within 712 m of the site of their previous year's nest site (if successful). This degree of philopatry is similar to that reported for Greater Sage-Grouse in Wyoming (Berry and Eng 1985) and Idaho (Fischer et al. 1993). Greater Sage-Grouse in Washington showed less philopatry to a previous year's successful nest location, moving an average of 1,600 m in the subsequent nesting season (Schroeder and Robb 2003).

The association between lek location and nest placement has important management implications for identifying critical nesting habitat. Bradbury (1981) hypothesized that female home ranges included only one lek and that >50% of all females should locate their nests nearer to that lek than other nearby leks. Studies of Greater Sage-Grouse and Sharp-tailed Grouse have provided support for this hypothesis (Bradbury et al. 1989, Giesen 1997). In Colorado and Minnesota, however, only 23 of 89 (26%; Schroeder 1991) and 7 of 18 (39%; Svedarsky 1988) Greater Prairie-Chickens nested closer to their lek of capture than to other leks, respectively. Similarly, in Idaho Wakkinen et al. (1992) found 92% of Greater Sage-Grouse nests within 3 km of a lek, but only 55% were within 3 km of the lek of capture. Our Lesser Prairie-Chicken nesting data also do not support Bradbury's (1981) hypothesis: 80% of our females (147 of 184) nested closer to a lek other than that on which they were captured. More importantly, we located >80% of all nests within 1 km of a known lek site; thus, we believe that providing secure nesting habitat within 1 km of a lek site is an important management strategy.

Our study provides the first comprehensive description of Lesser Prairie-Chicken nesting ecology in terms of age-specific reproductive effort. Our estimates of Lesser Prairie-Chicken nesting parameters should be viewed as approximations, however, because our methodology did not allow us to locate nests that were destroyed during the laying process. Nevertheless, our estimates provide a much better understanding of Lesser Prairie-Chicken demography in sand sagebrush habitats. The low nest success we observed (26%) is troubling, especially if ≥50% nest success is required for population stability (Westemeier 1979). Sensitivity analyses have revealed that nest success is one of the most influential demographic parameters affecting population growth of prairie grouse (Peterson and Silvy 1996, Wisdom and Mills 1997, Hagen 2003). Thus, habitat management designed to enhance nest success of Lesser Prairie-Chickens in southwestern Kansas should be a priority. Similar information on nesting ecology from Lesser Prairie-Chicken populations in other states and habitat types is needed to identify regional and site-specific conservation needs and to aid in the development of range-wide population models.

ACKNOWLEDGMENTS

We thank the private landowners of southwestern Kansas and the Sunflower Electric Power Corporation for property access. C. C. Griffin, G. C. Salter, T. G. Shane, T. L. Walker, Jr., and T. J. Whyte assisted with fieldwork. This study was supported by Kansas State University, Division of Biology; Kansas Agricultural Experiment Station (Contribution No. 04–411-J); Kansas Department of Wildlife and Parks; Federal Aid in Wildlife Restoration Projects W-47-R and W-53-R; and Westar Energy, Inc. Finally, we thank J. W. Connelly, M. A. Schroeder, and three anonymous reviewers for comments on earlier drafts of this manuscript.

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The Wilson Journal of Ornithology 118(1):36–41, 2006

A COMPARATIVE BEHAVIORAL STUDY OF THREE GREATER SAGE-GROUSE POPULATIONS

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ABSTRACT.—We compared male strut behavior of the genetically distinct Lyon, Nevada/Mono, California Greater Sage-Grouse (*Centrocercus urophasianus*) population with that of two proximal populations: Nye, Nevada, and Lassen, California. We measured strut rates and nine acoustic components of the strut display in all three populations. Male strut rates did not differ among populations. Acoustic components of the Lyon/Mono and Lassen populations were similar, whereas the Nye population was distinct. The genetically distinct Lyon/Mono population was more similar behaviorally to the Nye population than the genetically similar Nye and Lassen populations were to each other. Overall, the Lyon/Mono population did not exhibit detectable differences in male strut behavior. Reproductive isolation through sexual selection does not appear to have occurred in the Lyon/Mono population. *Received 27 September 2004, accepted 19 October 2005.*

Two recent studies based on mitochondrial gene sequence (Benedict et al. 2003, Oyler-McCance et al. 2005) and nuclear microsatellite markers (Oyler-McCance et al. 2005) revealed a genetically distinct population of Greater Sage-Grouse (*Centrocercus urophasianus*) on the Nevada/California border (Lyon, Nevada/Mono, California). Those studies indicated that the Lyon/Mono Greater Sage-Grouse population is more genetically distinct from other Greater Sage-Grouse populations than is the newly described (Young et al. 2000) Gunnison Sage-Grouse (*C. minimus*) species. Several factors, including the apparent genetic and geographic isolation of Lyon/Mono sage-grouse from other populations, the degradation and loss of sagebrush (*Artemisia* spp.) habitat, and an overall population decline, have made this a population of interest from both evolutionary and conservation perspectives.

Morphological (Hupp and Braun 1991) and behavioral studies (Young et al. 1994) of Gunnison Sage-Grouse provided evidence that sexual selection had driven speciation in the isolated populations of sage-grouse in southwestern Colorado and southeastern Utah. The use of both mitochondrial (Kahn et al. 1999) and nuclear markers (Oyler-McCance et al. 1999) supported the morphological and behavioral data and led to species designation for the Gunnison Sage-Grouse (American Ornithologists' Union 2000, Young et al. 2000). A similar approach would determine whether the genetic distinctiveness of the Lyon/Mono population has been manifested morphologically and/or behaviorally as it has in Gunnison Sage-Grouse. If so, it could potentially lead to a taxonomic reclassification.

Male mating success and mate-choice cues (Gibson and Bradbury 1985), territoriality (Gibson and Bradbury 1987), components of female choice (Gibson et al. 1991), and male strutting behavior (Young et al. 1994) have been studied previously in the Mono sage-grouse population. However, with the exception of Young et al. (1994), there have been no comparative studies among populations. Young et al. (1994) compared secondary sexual characteristics from male strut displays among three populations—one Gunnison Sage-Grouse population (Gunnison Basin, Colorado) and two Greater Sage-Grouse populations (Mono, California, and Jackson, Colorado). The structure of the Gunnison male strut display was strikingly different from that of the other two populations. However, the comparison of the similarly structured strut display between males from Mono and Jackson indicated statistically significant differences in most of the acoustic measures.

In light of the genetic distinctiveness of Lyon/Mono sage-grouse and the behavioral results of Young et al. (1994), we undertook a further examination of male strut display behavior. We compared the Lyon/Mono popu-

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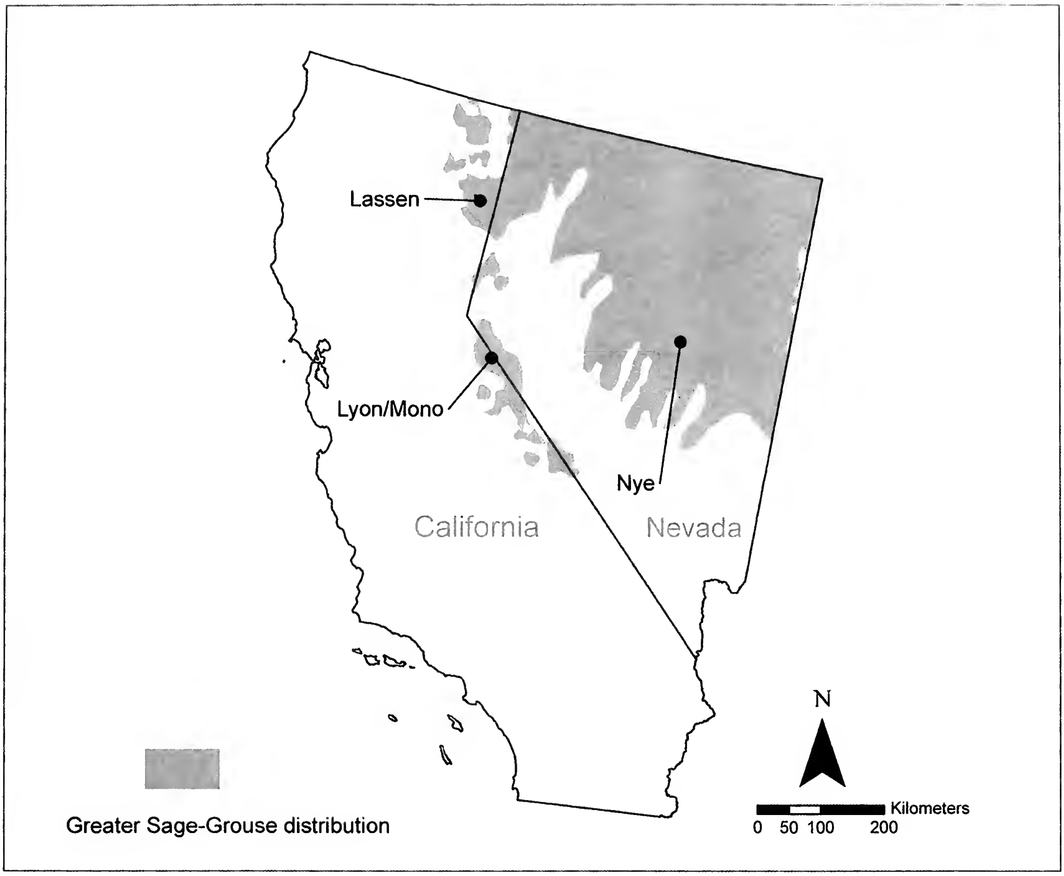

FIG. 1. Current Greater Sage-Grouse distribution in California and Nevada, and locations of three sample populations (modified from Schroeder et al. 2004).

lation with two proximal populations of Greater Sage-Grouse (Fig. 1). We tested the hypothesis that the Lyon/Mono population's behavior is measurably different from that of other Greater Sage-Grouse populations and may, in fact, be considered a separate taxon given the genetic differences. Alternatively, although the Lyon/Mono population appears genetically isolated, behaviorally it may not be significantly different from other Greater Sage-Grouse populations, indicating that sexual selection resulting in pre-mating isolating mechanisms has not occurred.

METHODS

The three populations we studied are from the southwestern edge of the Greater Sage-Grouse range in Nevada and California (Fig. 1). Behavioral measurements of male strut displays were taken at five leks. Greater Sage-Grouse in Lyon County, Nevada, and Mono County, California, form a connected, interbreeding population (Lyon/Mono). Recordings were completed between 9 and 17 April 2001 at three leks from the Lyon/Mono population: Lyon County, Nevada (Desert Creek 2 lek; 38° 42′ N, 119° 18′ W; 1,603 m), southern Mono County, California (Long Valley 1 lek; 37° 42′ N, 118° 48′ W; 2,124 m), and northern Mono County, California (Biedeman lek; 38° 12′ N, 119° 6′ W; 2,447 m). Of the three recorded Lyon/Mono leks, the Desert Creek and Biedeman leks are farthest apart (123 km). Lassen County, California (Eastside lek; 40° 18′ N, 120° 0′ W; 1,490 m), is approximately 250 km north and Nye County, Nevada (Roadside lek; 38° 42′ N, 116° 47′ W; 2,121 m), is approximately 215 km east of the

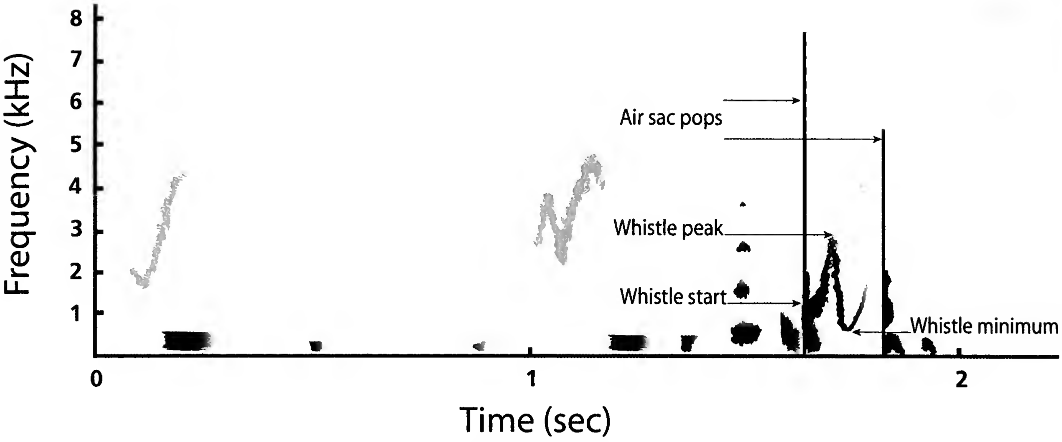

FIG. 2. Typical sonagram of a Greater Sage-Grouse male strut display. The two air sac pops, whistle start frequency, whistle peak, and whistle minimum are labeled. See Table 1 for all acoustic components (modified from Young et al. 1994).

Lyon/Mono population; recordings at these sites were completed between 3 and 11 April 2002. The number of males sampled from each of the five leks was as follows: Desert Creek 2 ($n = 6$), Long Valley 1 ($n = 9$), Biedeman ($n = 9$), Eastside ($n = 11$), and Roadside ($n = 14$); therefore, the sample size for the Lyon/Mono population was $n = 24$.

Males perform a ritualized strut display in which they take a few steps forward and brush their wings twice against their esophageal pouch producing loud swishing noises (Fig. 2). Following these wing movements, males compress air sacs and produce syringeal sounds to complete a single strut display (Hjorth 1970). Male strut displays were recorded and compared using the methods of Young et al. (1994) with the following modifications. Only adult males were monitored, and these were distinguished from juveniles in the field by the presence of a clear white upper breast on adults. Individual males were identified by their tail patterns (Wiley 1973). At least 15 struts per male were recorded using a Sony DCR TRV720 digital camcorder and a Sennheiser MKH70-P48 microphone. Sounds of individual struts were digitized at 22 kHz using Canary 1.2.4 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, New York).

We measured nine acoustic components (Table 1, Fig. 2) and calculated population means derived from individual male averages for each component. An estimate of repeatability ($[r = s^2_A/(s^2 + s^2_A)]$; Lessells and Boag 1987) was used to measure the proportion of within-individual variation within populations for each component. Repeatabilities range from 0 (low) to 1.0 (high). High repeatabilities indicate that the measured trait varies little within individuals relative to the population variation, suggesting that the trait could respond to sexual selection.

To calculate strut display rate, we timed between-strut intervals using Etholog 2.2, an ethological transcription tool (Ottoni 2000). The display rate for each male was based on 7–40 consecutive struts in which no more than 30 sec had lapsed between struts. Females were present on all leks during strut-rate measurements, but any male included in the strut-rate analyses had to have females within 20 m of them during recording. This criterion lowered the sample sizes (number of males) for population strut-rate estimation (Fig. 3). At the Lassen and Lyon leks, measurements were taken as one female moved throughout the leks. The southern Mono, northern Mono, and Nye leks all had multiple females visiting leks over the various days that measurements were taken.

We used analysis of variance (ANOVA) to assess differences among populations for each acoustic component and strut rate. We then used the GT2-method (Hochberg 1974) to make unplanned comparisons among popula-

TABLE 1. Nine measured acoustic components of male Greater Sage-Grouse strut display in three populations from Nevada and California. Males were recorded while strutting during spring 2001 and 2002.

		Lyon, Nevada/Mono, California ($n = 24$)		Lassen, California ($n = 11$)		Nye, Nevada ($n = 14$)		
Measured variable	Acoustic component	Mean	SE	Mean	SE	Mean	SE	P^a
First pop to whistle peak (msec)	1	73.41	0.37	73.85	0.65	70.30	0.52	<0.001
Whistle peak to whistle minimum (msec)	2	40.21	0.28	39.81	0.32	41.69	0.61	0.012
Pop to pop (msec)	3	199.89	0.73	199.64	0.97	192.24	0.88	<0.001
Whistle start frequency (Hz)	4	861.17	7.61	861.65	10.97	930.19	20.19	<0.001
Whistle peak (Hz)	5	2,619.83	21.06	2,657.32	23.09	2,873.84	42.85	<0.001
Whistle minimum (Hz)	6	533.58	5.89	514.48	7.56	637.26	9.63	<0.001
Whistle start to peak difference (Hz)	7	1,771.61	20.69	1,795.22	23.94	1,944.72	35.09	<0.001
Whistle peak to minimum difference (Hz)	8	2,096.48	21.90	2,151.64	17.61	2,241.51	39.14	0.002
Whistle start to minimum difference (Hz)	9	333.90	11.33	353.70	13.99	290.38	16.80	0.020

[a] ANOVA.

tion means with unequal sample sizes for acoustic components. This method uses the studentized maximum modulus distribution *m* to compute a minimum significant difference (MSD). The significance level for the ANOVA was set at $P = 0.05$ and for the GT2-method it was lowered from $P = 0.05$ to $P = 0.017$ using a Bonferroni correction ($\alpha'' = \alpha/k$; Sokal and Rohlf 1995) for multiple tests. We used $\alpha'' = 0.01$ when referring to the studentized maximum modulus *m* critical values table (GT2-method).

RESULTS

All nine acoustic components of the strut display differed among populations (ANOVA, all $P < 0.05$; Table 1). The acoustic components of the males' displays were similar between Lyon/Mono and Lassen, whereas those of Nye males' displays were consistently distinct from those of the other two populations. Nye differed from both Lyon/Mono and Lassen for acoustic components 1 and 3–7 (GT2-test, all $P < 0.01$). For component 8, Nye differed only from Lyon/Mono (GT2-test, $P < 0.010$). All other pairwise population comparisons for minimum significant differences were not significant (GT2-test, all $P > 0.01$).

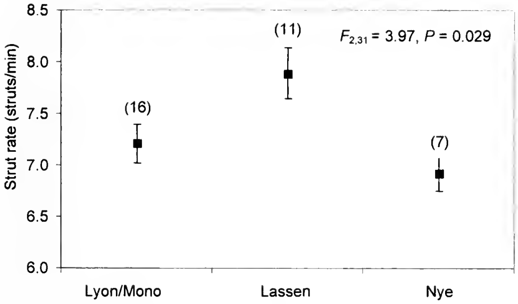

FIG. 3. Means (with standard error bars) and ANOVA result for strut rates of male Greater Sage-Grouse from three populations: Lyon, Nevada/Mono, California; Lassen, California; and Nye, Nevada. Sample sizes (number of males) are in parentheses.

Repeatability estimates of the acoustic components ranged from 0.41 to 0.84 in Lassen, 0.57 to 0.96 in Nye, and 0.35 to 0.91 in Lyon/Mono (Table 2). The highest repeatability estimate for all three populations was for whistle peak (component 5).

Strut rates (struts/min) differed ($F_{2,31} = 3.97$, $P = 0.029$) among populations (Fig. 3). However, pairwise comparisons between populations indicated that none were significant (GT2-test, all $P > 0.01$). Lassen males had the highest strutting rate (7.84 struts/min), whereas males from Nye had the lowest strutting rate (6.92 struts/min). Lyon/Mono males had an intermediate strutting rate (7.21 struts/min).

DISCUSSION

We measured behavioral traits and secondary sexual characteristics that are related to sexual selection in sage-grouse, which could

TABLE 2. Repeatability estimates of strut display acoustic components within individual males from three Greater Sage-Grouse populations in California and Nevada. Males were recorded while strutting during spring 2001 and 2002.

Acoustic component	Lyon, Nevada/ Mono, California *n* = 24	Lassen, California *n* = 11	Nye, Nevada *n* = 14
1	0.51	0.78	0.65
2	0.35	0.44	0.62
3	0.64	0.74	0.65
4	0.57	0.67	0.79
5	0.91	0.84	0.96
6	0.57	0.68	0.79
7	0.53	0.80	0.88
8	0.74	0.49	0.87
9	0.41	0.41	0.57

therefore lead to divergence. Based on behavioral differences in male strut displays, our study did not support the idea that the genetically distinct Lyon/Mono population should be considered for separate taxonomic status. The Lyon/Mono and Lassen populations were similar to each other, while the Nye population was the most unique across nine acoustic components of male mating displays. However, across six components (1–4, 6, 9), the Nye versus Lassen populations were either more different or as different as Nye versus Lyon/Mono populations (Table 1). Even though the Lyon/Mono population is genetically distinct, male mating behaviors are more similar to those of the Nye population than those of the genetically similar Nye and Lassen populations are to each other (Table 1).

The repeatability estimates generally varied widely across populations. However, three acoustic components (3, 5, and 9) were relatively comparable among the three populations. The high repeatability estimates for components 3 (pop to pop) and 5 (whistle peak) indicate that these traits vary little within individual males relative to the variation within populations and could potentially respond to selection. Young et al. (1994) also found high repeatability estimates for whistle peak, which has been shown to be related to female mate choice (Gibson and Bradbury 1985, but see Gibson et al. 1991). A low repeatability for component 9 (whistle start to minimum difference) is most likely the result of high levels of variability within individuals rather than a lack of genetic variation or inaccuracies in measurement (Boake 1989). Nye had the highest repeatability estimates for seven of the nine acoustic components, suggesting low variation in the acoustic measurements, despite samples being taken across several days with multiple females being present.

Although strut rates did differ among populations, pairwise comparisons of strut rate did not differ statistically between populations. This result agrees with the observations of Young et al. (1994), who found that strut rates did not differ between two Greater Sage-Grouse populations—Mono, California, and Jackson, Colorado. Strut rates may vary with time of day, time of season, and proximity of females (R. M. Gibson pers. comm.); therefore, variation in strut rate within and between males may outweigh differences in strut rates among populations except in strong cases of population divergence.

Our results suggest that the Lyon/Mono population does not exhibit any appreciable behavioral differences in male mating displays from other Greater Sage-Grouse populations. The Lyon/Mono population is significantly different genetically from the Lassen population (Benedict et al. 2003, Oyler-McCance et al. 2005), yet behaviorally, the Lyon/Mono and Lassen populations have similar acoustic strut components and strut rates. The implications of the slight behavioral differences observed in the Nye population on female mate choice may be determined upon further behavioral observations that include additional leks, years, and populations. It is possible that there are measurable differences in acoustic components of the strut display between most populations, but these differences are generally minimized by gene flow.

The Lyon/Mono population is genetically more diverse and distinct than the Gunnison Sage-Grouse species (Kahn et al. 1999, Oyler-McCance et al. 1999, Benedict et al. 2003, Oyler-McCance et al. 2005). Using mitochondrial DNA sequence, Benedict et al. (2003) estimated that the Lyon/Mono population has been isolated from other Greater Sage-Grouse populations for tens of thousands of years. Yet, neither local adaptation to ecological or environmental factors, nor genetic drift, nor sexual selection has led to detectable phenotypic (behavioral) differences in this population. Reproductive isolation does not appear to have occurred through sexual selection in the Lyon/Mono population as it has in the Gunnison Sage-Grouse species.

ACKNOWLEDGMENTS

Funding and support for this project was provided by the California Department of Fish and Game, Quail Unlimited, the National Fish and Wildlife Foundation, Western State College of Colorado, and the Bureau of Land Management. We are grateful to D. S. Blankenship, F. A. Hall, T. L. Russi, J. Fatooh, S. L. Nelson, R. M. Gibson, W. F. Mandeville, and T. Slatauski for logistical and field support. We appreciate M. K. Bollig and M. D. Kascak for their assistance with graphics. We thank C. E. Braun, J. W. Connelly, R. M. Gibson, S. J. Oyler-McCance, K. P. Reese, and J. St. John for helpful comments on the manuscript. Finally, we thank S. L. Thode and R. D. Taylor for patience and support.

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The Wilson Journal of Ornithology 118(1):42–52, 2006

FIRST KNOWN SPECIMEN OF A HYBRID *BUTEO*: SWAINSON'S HAWK (*BUTEO SWAINSONI*) × ROUGH-LEGGED HAWK (*B. LAGOPUS*) FROM LOUISIANA

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ABSTRACT.—We report a specimen that appears to be a hybrid between Swainson's Hawk (*Buteo swainsoni*) and Rough-legged Hawk (*B. lagopus*), which, to our knowledge, is the first hybrid specimen for the genus. There are few reports of hybridization between *Buteo* species, most of which have been observations of interspecific nesting pairs. The specimen described herein was collected in Louisiana and initially identified as a Rough-legged Hawk because of its feathered tarsi and the dark bellyband and carpals. A DNA sequence from the maternally inherited mitochondrial ND6 gene was identical to a published sequence for Swainson's Hawk. Nuclear DNA sequences from two introns contained only five variable sites among a panel of five potential parental taxa, but the hybrid sequence was most consistent with parentage by Rough-legged and Swainson's hawks. The feathered tarsi of the hybrid strongly suggested that the father was either a Rough-legged or Ferruginous hawk (*B. regalis*), the only North American raptors other than Golden Eagle (*Aquila chrysaetos*) that have feathered tarsi. Plumage and size characters were inconsistent with those of Ferruginous Hawk, and, other than the darkly pigmented leg feathers, were intermediate between the light morphs of Swainson's and Rough-legged hawks. The breeding range of Swainson's Hawk in Alaska and northern Canada is poorly known, but it overlaps that of the Rough-legged Hawk in at least a few locations, albeit at low densities, which may be a factor in hybridization. The occurrence of this hybrid is evidence of the potential for interbreeding between North American members of the genus *Buteo*, most of which are genetically closely related. Such hybridization could have implications for genetic diversity, adaptation, or the evolution of reproductive barriers. In any case, such hybrids present field and museum identification problems. *Received 6 December 2004, accepted 3 October 2005.*

Few documented cases of hybridization exist between any 2 of the 27 or so species in the genus *Buteo*. Hybrid combinations have been reported for Long-legged Buzzard (*B. rufinus*) and Upland Buzzard (*B. hemilasius*) in Asia (Pfander and Schmigalew 2001), Common Buzzard (*B. buteo*) and Long-legged Buzzard in Europe (Dudás et al. 1999), and Red-shouldered Hawk (*B. lineatus*) and Gray Hawk (*Asturina nitidus*) in North America (Lasley 1989). Additionally, an adult Swainson's Hawk (*B. swainsoni*) bred for more than 8 years with a presumably escaped South American Red-backed Hawk (Red-backed Buzzard, *B. polyosoma*) in Colorado, USA, and produced offspring in some years (Allen 1988, Wheeler 1988); a Red-tailed Hawk (*B. jamaicensis*) that escaped from a falconer bred with a Common Buzzard in Scotland (Murray 1970). However, to our knowledge, there are no museum specimens of the offspring of such unions. Thus, it was with great interest that we found a specimen of an apparent hybrid in the Louisiana State University Museum of Natural Science (LSUMNS), Baton Rouge. It is a juvenile male, has feathered tarsi and mostly dark carpal patches, was collected near Baton Rouge, Louisiana, and was identified as a Rough-legged Hawk (*B. lagopus*). Its plumage appears almost the same as that of a probable hybrid between the same two species, first seen and photographed in November 2002 by Martin Reid near Ft. Worth, Texas; WSC observed and took photos of that bird in January 2003.

Herein we present a description of the putative hybrid *Buteo* based on its morphology, plumage, and mitochondrial and nuclear DNA sequences. A comparison of the hybrid to a set of potential parental *Buteo* taxa led to the conclusion that it descended from the mating of a female Swainson's Hawk with a male Rough-legged Hawk. Although not shown on some published range maps, Swainson's Hawks breed sparsely throughout at least a part of the Rough-legged Hawk's breeding range in far-northern North America.

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METHODS

WSC noted that the specimen, LSUMZ 159785, which was stored with a handful of juvenile light-morph Rough-legged Hawks, differed from them and was much like a presumed hybrid he had seen and photographed near Ft. Worth, Texas in January 2003. After a comparison of this specimen with those of juvenile Rough-legged and Swainson's hawks, he determined that it might be a hybrid. The specimen had been collected on 4 November 1994 in East Baton Rouge Parish, Highway 30 at Burtville, Louisiana, by S. W. Cardiff and D. L. Dittmann. A tissue sample was deposited in the LSUMNS Collection of Genetic Resources (catalog No. B23743). The specimen was sexed internally as a male (left testis 7 × 11 mm) and was in juvenal plumage; the skull was 75% ossified.

We used a DNEasy tissue kit (Qiagen, Valencia, California) to extract DNA from frozen muscle tissue of the putative hybrid specimen, and one specimen of each of the following taxa: Rough-legged Hawk, Swainson's Hawk, Red-tailed Hawk, Harlan's Red-tailed Hawk (*B. jamaicensis harlani*), and Ferruginous Hawk. We amplified the mitochondrial ND6 gene for the hybrid specimen in 25 μl PCR reactions using Amplitaq Gold (Applied Biosystems [ABI], Foster City, California) with the primers tPROfwd and tGLUrev (Haring et al. 1999). For all six specimens, we amplified two nuclear loci, as follows: (1) intron 5 and flanking exon regions of the cytosolic adenylate kinase gene (AK1) using the primers AK5b+ and AK6c- (Shapiro and Dumbacher 2001), and (2) intron 3 and flanking exon regions of the Z-chromosome-linked muscle-specific receptor tyrosine kinase gene (MUSK) using primers designed by F. K. Barker: MUSK-E3F (CTTCCATGCACTAC AATGGGAAA) and MUSK-E4R (CTCTGA ACATTGTGGATCCTCAA). Standard PCR reactions were run on an MJ Research PTC-200 thermal-cycler under the following temperature regime: initial denaturation at 95° C for 8 min; 35 cycles of 92° C for 20 sec, 55° C for 60 sec, 72° C for 60 sec; and a final extension at 72° C for 10 min. For MUSK, the annealing temperature was adjusted to 50° C. Negative control reactions were used for all extractions and PCR to insure against contamination. PCR products were purified using a Qiagen Gel Extraction Kit (Qiagen, Valencia, California). Cycle-sequencing reactions were carried out in both directions using the primers described above in quarter- or sixteenth-volume reactions with a Big Dye Terminator Cycle Sequencing Kit (ver. 2 or 3.1, ABI). Cycle-sequencing products were purified using Sephadex columns. Purified samples were electrophoresed on an ABI 377 or 3100 automated sequencer. Sequences were assembled and edited using Sequencher 4.2.2 (Gene Codes Corporation, Ann Arbor, Michigan). The ND6 sequence was compared with published sequences for various *Buteo* species (Riesing et al. 2003).

We compared morphology and plumage of the hybrid to a panel of five potential parental taxa. We followed the "contradictory characters" approach of Rohwer (1994) to eliminate potential pairs of parental taxa for which characters of the presumed hybrid fall outside of the range of variation. We assembled standard measurements of body mass, wing chord (unflattened), exposed culmen, and hallux (Baldwin et al. 1931) for juvenile males of potential paternal taxa from banding data for Swainson's, Rough-legged, and eastern Red-tailed hawks (*B. j. borealis*), and from museum specimen data for western Red-tailed (*B. j. calurus*), Harlan's Red-tailed, and Ferruginous hawks. We performed two stepwise discriminant function analyses with these four morphological variables using SPSS ver. 11.5 (SPSS, Inc. 2002). In both stepwise analyses, we used 0.05 probability of *F* for entry and 0.10 probability of *F* for removal of each variable, set equal prior probabilities of group membership, and used within-group covariance matrices. The three Ferruginous Hawk specimens were not included in the analysis due to small sample size, and the single Harlan's Red-tailed Hawk individual was included in the western Red-tailed Hawk group. The first discriminant function analysis included Rough-legged, Swainson's, eastern Red-tailed, and western Red-tailed hawks as groups. All four morphological variables were significant and included in the final model, and three significant discriminant functions were generated. The putative hybrid individual and the three Ferruginous Hawks were then classified using these discriminant functions. In the second discriminant function analysis, we only included Rough-legged and Swainson's hawks as groups. Only mass, wing chord, and culmen were significant and included in the final model, and only one discriminant function explained 100% of the variation between the two groups. The putative hybrid was then again classified according to this discriminant function. To account for possible shrinkage of museum specimens relative to live birds (Winker 1993), we repeated all analyses under the assumption of a 3% reduction in size due to drying. The adjustment for shrinkage had no substantive effect on the results. Finally, with respect to plumage characters, we compared the specimen with juvenile male Swainson's and Rough-legged hawks, including pigmentation of the head, upperparts, breast, belly, tail, and legs, and emargination of the seventh primary (P7).

RESULTS

The mitochondrial DNA sequence of the putative hybrid, totaling 558 bp, was an identical match to a published sequence from a Swainson's Hawk collected in New Mexico (Table 1; GenBank accession No. AY213028). The sequence was 0.76% divergent from its nearest relative, the Galapagos Hawk (*B. galapagoensis*), and 3.23–3.58% divergent from the only sympatric congeners: Red-tailed, Ferruginous, and Rough-legged hawks (Clark and Wheeler 2001, Riesing et al. 2003; Table 1). Mitochondrial haplotypes are shared between mothers and their offspring because the mitochondrial genome is non-recombining and maternally inherited (Lansman et al. 1983). The identical mtDNA sequences of the specimen and a known Swainson's Hawk strongly suggests that the maternal parent was a Swainson's Hawk.

The nuclear AK1 sequence of the putative hybrid, totaling 542 bp, was identical to sequences from the Swainson's, Rough-legged, eastern Red-tailed, Harlan's, and Ferruginous hawks. The complete lack of variation at this locus prevents the elimination of any of these taxa as potential parents. The nuclear MUSK sequence, totaling 599 bp, contained five variable sites for the six taxa included in this study (Table 2). Among the five variable sites was a substitution unique to the Ferruginous Hawk sample (T; site no. 480), and another

TABLE 1. Uncorrected percent DNA sequence divergence between the presumed *Buteo* hybrid and potential parental *Buteo* taxa at mitochondrial (ND6) and nuclear (AK1 and MUSK) loci, with GenBank accession numbers. The mtDNA of the hybrid matches that of Swainson's Hawk, and the nuclear introns are most similar to those of Swainson's and Rough-legged hawks.

Species	Source	ND6 GenBank no.	ND6 % divergence from hybrid	AK1 GenBank no.	AK1 % divergence from hybrid	MUSK GenBank no.	MUSK % divergence from hybrid
Hybrid	LSUMZ[a] B23743	DQ101251	—	DQ101247	—	DQ101254	—
B. swainsoni	Riesing et al. 2003	AY213028	0.00	—	—	—	—
B. swainsoni	LSUMZ B23587	—	—	DQ101248	0.00	DQ101257	0.00
B. swainsoni	Shapiro and Dumbacher 2001	—	—	AF307892	0.00	—	—
B. lagopus	Riesing et al. 2003	AY213017	3.23	—	—	—	—
B. lagopus	LSUMZ B8683	—	—	DQ101245	0.00	DQ101255	0.00
B. regalis	Riesing et al. 2003	AY213018	3.58	—	—	—	—
B. regalis	LSUMZ B26245	—	—	DQ101249	0.00	DQ101255	0.17
B. jamaicensis borealis	Riesing et al. 2003	AY213019	3.23	—	—	—	—
B. jamaicensis borealis	LSUMZ B33264	—	—	DQ101250	0.00	DQ101253	0.17
B. jamaicensis harlani	LSUMZ B23470	—	—	DQ101246	0.00	DQ101252	0.17

[a] Louisiana State University Museum of Natural Science, Baton Rouge.

TABLE 2. Variable sites on the 599 bp MUSK gene sequence for the presumed *Buteo* hybrid and five other buteos. The sites span part of exon 3, the entire intron 3, and part of exon 4, corresponding to positions 1311922–1312509 of the *Gallus gallus* chromosome Z genomic contig (GenBank NW 060751). Both states (i.e., A/T and A/G) are reported for heterozygous sites, as inferred by unambiguous double peaks on chromatograms.

	Variable position				
	65	113	157	452	480
Hybrid	A/T	A/G	C	A/G	C
Swainson's Hawk	T	A	C	G	C
Rough-legged Hawk	A/T	A/G	C	G	C
Ferruginous Hawk	T	A	C	G	T
Eastern Red-tailed Hawk	T	A	T	G	C
Harlan's Red-tailed Hawk	T	A	T	G	C

that was shared only by the eastern Red-tailed and Harlan's Red-tailed hawks (T; site no. 157). At two other sites (nos. 65 and 113), the Rough-legged Hawk and the hybrid were both heterozygous (A/T and A/G), with one exclusively shared state and one state in common with all other taxa (Table 2). The fifth variable site (no. 452) was heterozygous in the hybrid specimen only. Heterozygotes were inferred when chromatograms showed strong signal and unambiguous double peaks of nearly equal height.

We identified the paternal parent using phenotypic characters. Red-tailed Hawk, including Harlan's Hawk, can be eliminated as the putative father because it always has unfeathered tarsi. It seems unlikely that two species with bare tarsi would produce a hybrid with feathered tarsi. Further, the Red-tailed Hawk's culmen is considerably larger than that of the hybrid (Table 3). Finally, juvenile Red-tailed Hawks share few plumage characters with the hybrid (Wheeler and Clark 1995, Clark and Wheeler 2001); we would not expect, for example, a hybrid Red-tailed Hawk × Swainson's Hawk juvenile to have the heavy, dark bellyband (Fig. 1) or the dark carpal patches of the hybrid.

Both Ferruginous and Rough-legged hawks have feathered tarsi and are the most likely paternal candidates of the hybrid specimen. However, Ferruginous Hawks have noticeably wider gapes (Bechard and Schmutz 1995) and longer bills, wings, and halluces than the hybrid (Table 3). The measurements of the hybrid are far closer to those of Swainson's Hawk than to Ferruginous Hawk, suggesting that the bird is not intermediate in size as would be expected in an F1 hybrid between these two species. In contrast, the measurements for body mass and wing chord are intermediate between juvenile male Swainson's

TABLE 3. Comparison of measurements (mean ± SE) of the hybrid *Buteo* specimen with juvenile male Rough-legged, Swainson's, Ferruginous, eastern Red-tailed, western Red-tailed, and Harlan's Red-tailed hawks. Body mass and wing chord of the hybrid are intermediate between Rough-legged and Swainson's hawks. Culmen and hallux are closest to Swainson's Hawk.

	n	Body mass (g)	Wing chord (mm)	Culmen (mm)	Hallux (mm)
Hybrid	1	702.0	381.0	19.3	21.4
Swainson's Hawk[a]	20	638.3 ± 16.8	378.5 ± 2.4	21.4 ± 0.3	21.7 ± 0.4
Rough-legged Hawk[b]	39	860.8 ± 12.6	398.2 ± 1.6	21.5 ± 0.1	23.9 ± 0.2
Ferruginous-Hawk[c]	3	1,091.4 ± 14.3	413.7 ± 1.8	25.0 ± 0.3	25.6 ± 0.3
Eastern Red-tailed Hawk[d]	24	825.4 ± 15.8	351.8 ± 1.9	27.2 ± 0.2	24.1 ± 0.2
Western Red-tailed Hawk[e]	12	905.5 ± 30.3	374.4 ± 2.9	24.2 ± 0.3	27.7 ± 0.4
Harlan's Red-tailed Hawk[f]	1	932.0	365.0	23.5	26.0

[a] Unpublished banding data from Texas and New Jersey, sex determined by size.
[b] Unpublished banding data from New York, sex determined by size.
[c] MVZ (Museum of Vertebrate Zoology, University of California, Berkeley) specimen data from California.
[d] Unpublished banding data from New Jersey, sex determined by size.
[e] MVZ specimen data from British Columbia, California, Arizona, New Mexico, and Nevada.
[f] MVZ specimen data from British Columbia.

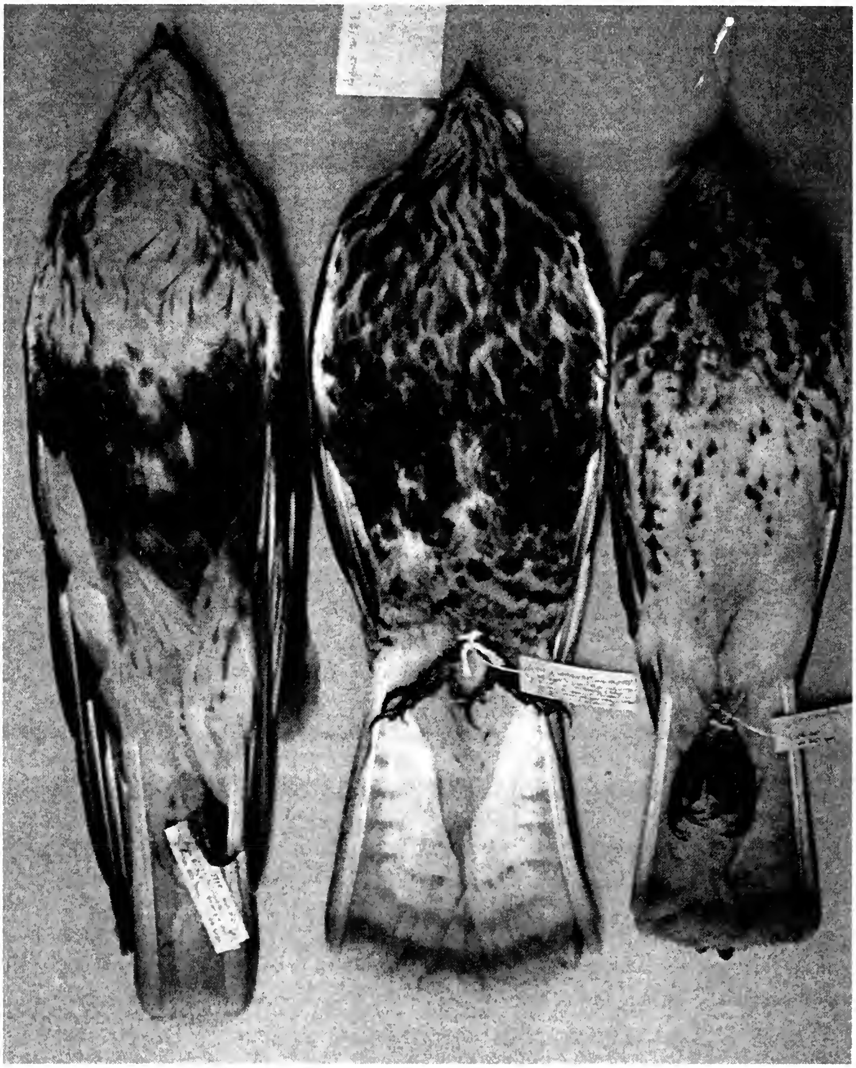

FIG. 1. Specimens showing ventral view of the hybrid *Buteo* (center), compared with juvenile male Rough-legged Hawk (left) and juvenile male Swainson's Hawk (right). Characters of the hybrid are intermediate.

and Rough-legged hawks (Table 3). Finally, the plumage characters of both light- and dark-morph juvenile Ferruginous Hawks do not match those of the specimen (Wheeler and Clark 1995, Clark and Wheeler 2001); a hybrid Ferruginous Hawk × Swainson's Hawk juvenile, for example, would not be expected to have the dark bellyband (Fig. 1) nor the dark carpal patches of the hybrid.

Most plumage characters of the hybrid specimen are similar to those of juvenile male Swainson's or Rough-legged hawks, or intermediate between them (Figs. 1–2, Table 4). The notching of P7 is also intermediate (Fig. 3). This feather has a noticeable abrupt widening or "notch" on the trailing edge for Rough-legged Hawk (same for Ferruginous and Red-tailed hawks) but not for Swainson's Hawk. The widening begins 93 mm from the tip on a juvenile male specimen Rough-legged Hawk (Fig. 3A), widening about 15 mm at an angle of 70° to the feather shaft. P7 on a juvenile male Swainson's Hawk specimen began widening gradually 47 mm from the tip and lacked a distinctive notch (Fig. 3B). The hybrid's P7 began widening 59 mm from the

FIG. 2. Specimens showing dorsal view of the hybrid *Buteo* (center), compared with juvenile male Rough-legged Hawk (left), and juvenile male Swainson's Hawk (right). Characters of the hybrid are intermediate.

tip with a notch and widened about 9 mm at a 60° angle (Fig. 3C).

In the first discriminant function analysis, which included Rough-legged, Swainson's, eastern Red-tailed, and western Red-tailed hawks as groups, the first two discriminant functions explained 96.2% of the variation between the groups (Fig. 4A). The first function correlated strongly with culmen (r = 0.651) and wing chord (r = −0.513) and explained 80.1% of the variance. The second function correlated strongly with hallux (r = 0.814) and body mass (r = 0.646) and explained 16.1% of the variance. Using both functions, the hybrid was classified as a Rough-legged Hawk with 31.2% probability, as a Swainson's Hawk with 68.8% probability, and as an eastern or western Red-tailed Hawk with 0% probability. In the second discriminant function analysis, which included only Rough-legged and Swainson's hawks as groups, one discriminant function explained 100% of the variation between the groups (Fig. 4B). This function correlated strongly with mass (r = 0.875) and wing chord (r = −0.580). Using this function, the hybrid was classified as a

TABLE 4. Comparison of plumage characters of the hybrid *Buteo* specimen with juvenile male Rough-legged and Swainson's hawks. Characters of the hybrid are intermediate or like one or the other of the parent species.

Character	Rough-legged Hawk	Swainson's Hawk	Hybrid
Crown	Pale	Dark	Dark, pale streaks
Superciliary	None	Rufous	Buffy
Malar	Narrow	Wide	Wide
Back feathers	Brown, pale sides	Dark brown, pale tips	Dark brown, pale tips and sides
Breast	Lightly streaked	Heavily streaked	Heavily streaked
Belly	Solidly dark	Buffy	Dark with pale edges
Legs	Feathered, lightly marked	Bare	Feathered, darkly marked
Uppertail	White base, dusky tip, no bands	Gray-brown, dark bands	Narrow white base, gray-brown, dark bands
Primary, outer web	Grayish cast	Dark	Grayish cast
Primary, inner web	Pale, no barring	Darker, barring	Pale, barring

Rough-legged Hawk with 45.4% probability and as a Swainson's Hawk with 54.5% probability.

DISCUSSION

Based on mtDNA, we conclude that the mother of this putative hybrid is a Swainson's Hawk. The most likely paternal candidates are raptors with feathered tarsi, Rough-legged and Ferruginous hawks. The latter was eliminated because of its plumage characters, much larger size, and unique MUSK intron haplotype.

Independent lines of evidence converged on the identification of the specimen as a hybrid between Swainson's and Rough-legged hawk. The combination of morphological and molecular characters, as in the diagnosis of a hybrid manakin (*Ilicura* × *Chiroxiphia*) by Ma-

FIG. 3. Notching of primary 7. (A) Rough-legged Hawk, (B) hybrid, and (C) Swainson's Hawk. The posterior margin of each P7 is highlighted in white. (Scale is not the same on each figure.) The shape of P7 of the hybrid is intermediate and unlike those of any *Buteo* species.

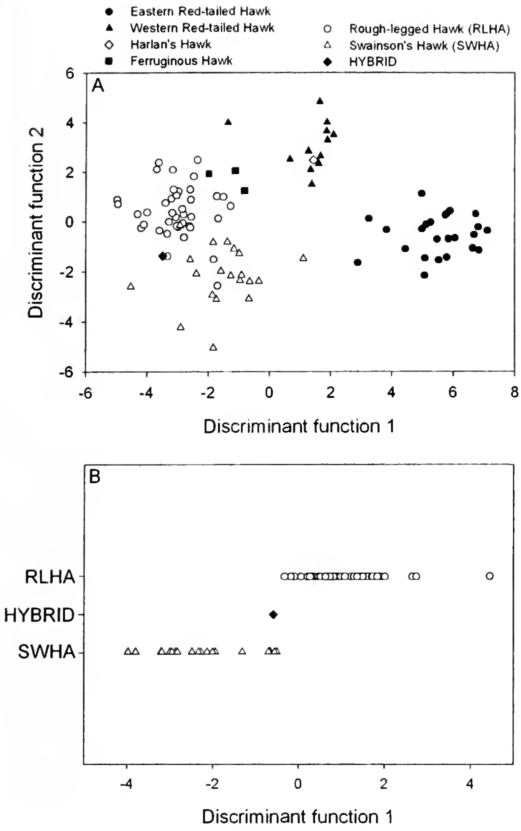

FIG. 4. Discriminant function analyses comparing juvenile males of *Buteo* species. In panel (A), plots of points along the first two significant discriminant functions are from an analysis that included Rough-legged, Swainson's, eastern Red-tailed, and western Red-tailed hawks as groups. These two discriminant functions explained 96.2% of the variation between the groups. The Harlan's Hawk was included in the western Red-tailed Hawk group, but was plotted with a unique symbol. The hybrid individual and three Ferruginous Hawks were then classified and plotted using these discriminant functions. In panel (B), points are plotted according to a discriminant function from an analysis that only included Rough-legged and Swainson's hawks as groups. One discriminant function explained 100% of the variation between the two groups. The hybrid was classified and plotted according to this discriminant function.

rini and Hackett (2002), is a powerful method for the identification of avian hybrids. In particular, the comparison of a single mtDNA sequence to the growing database of published sequences is an outstanding tool for identification of the maternal parent. In this case, the mtDNA sequence of the hybrid strongly suggests that its maternal parent was a Swainson's Hawk. The mother could have been a species other than Swainson's Hawk only if the mitochondrial identity were a mere artifact of incomplete lineage sorting. We consider this possibility unlikely because the mitochondrial study of Riesing et al. (2003) demonstrated that geographically heterogeneous samples of five Rough-legged, two Ferruginous, nine Red-tailed, and three Swainson's hawks are each reciprocally monophyletic, and the divergence levels between Swainson's Hawk and each of its sympatric congeners are greater than 3%.

The paucity of variation in the two nuclear introns illustrates the difficulty of using nuclear DNA to diagnose hybrids among closely related species. Intraspecific variation and lack of lineage sorting pose significant challenges to the conclusive identification of hybrid individuals, and these problems are compounded when potential parental taxa cannot be thoroughly sampled at the population level. Despite these difficulties, our sample of a single individual for each potential parental taxon yielded some variation that was consistent with the identification of Rough-legged Hawk as the paternal species. The eastern Red-tailed, Harlan's Red-tailed, and Ferruginous hawk samples each contained single substitutions on the MUSK intron that were not found in the hybrid. In contrast, only the Swainson's and Rough-legged hawk samples were completely compatible with parentage of the hybrid. Importantly, two heterozygous positions in the hybrid each contained a state that was shared exclusively with the Rough-legged Hawk sample.

Plumage and morphological characters of the hybrid specimen were generally intermediate between those of juvenile males of the parent species. This pattern is born out by the discriminant function analyses and is consistent with the characters of hybrids between other species of birds (e.g., Graves 1990, Rohwer 1994, Marini and Hackett 2002). However, the coloration of the tarsi feathers was not intermediate. Juvenile male Rough-legged Hawks have buffy tarsal feathers with sparse, dark markings, whereas Swainson's Hawks have bare tarsi. The hybrid specimen has tarsal feathers with heavy, dark barring, clearly not intermediate. The expectation that hybrid traits fall within the range of traits expressed by the parental taxa is based on the assumption that most traits are additive and polygenic (Falconer 1989) and is implicit in most hybrid diagnoses. Nonetheless, hybrids can also express traits that are extreme relative to those of the parental taxa (Rieseberg et al. 1999). It is possible that the darkly pigmented tarsal feathers could be one such transgressive trait, caused by complementary gene action, overdominance, or epistasis. Swainson's and Rough-legged hawk populations are known to possess genetic variation that results in differences in the quantity and distribution of melanin-based plumage pigments (Clark and Wheeler 2001). Rohwer (1994) reported other examples of characters that were not intermediate between those of the parental species. The culmen, and, to a lesser degree, the hallux of the hybrid were slightly smaller than our Swainson's and Rough-legged hawk measurements for those characters, providing another potential example of a non-intermediate character. However, specimen shrinkage could at least partly account for this difference.

The Swainson's Hawk breeds in an unknown amount of the breeding range of the Rough-legged Hawk in far northwestern North America. This is the extreme northern periphery of their distribution, and they occur at very low densities in taiga habitat where they are sympatric with the Rough-legged Hawk (England et al. 1997, Bechard and Swem 2002, Sinclair et al. 2003). This could increase the possibility that a female Swainson's Hawk could fail to find a conspecific mate. Given the broad overlap in distribution between Swainson's, Red-tailed, and Ferruginous hawks, the lack of documented instances of hybridization or interspecific pairings between any two of these three species suggests behavioral barriers to reproduction. Such barriers may not exist between Swainson's and Rough-legged hawks, which overlap only marginally and may have come into sympatry only recently. This hybrid pairing is consistent with the model of Short (1969), who proposed that hybridization is most likely to occur at the edges of a species' range.

Swainson's Hawks are rare during November in the area where the hybrid individual was found; there is only one November record for East Baton Rouge Parish, despite intensive coverage by birdwatchers and collectors (LSUMNS data). Although Lowery (1974) indicated that Rough-legged Hawk is a regular winter visitor to Louisiana, and several subsequent sight-based reports lacking photos have been accepted by the Louisiana Bird Records Committee, the only physical evidence substantiating the occurrence of a Rough-legged Hawk in Louisiana is a specimen collected on 12 March 1933 at Grand Isle (LSUMZ 4803). The present hybrid occurred at a place (and time) unexpected for either species—Rough-legged Hawks should occur farther north and Swainson's Hawks farther south. This intermediate migratory behavior, as well as a myriad of other ecological differences between Swainson's and Rough-legged hawks, suggests potential sources of reduced fitness in hybrids. Hybridization can provide a mechanism for gene flow between species, particularly if hybrids are interfertile with parental species and do not suffer reduced fitness (Arnold 1992). Alternatively, hybrid unfitness can reinforce behavioral pre-mating barriers through natural selection (Saetre et al. 1997), particularly in taxa such as Swainson's and Rough-legged hawks that may have recently come into secondary contact.

Hybrids between raptor species are reported infrequently, most likely because they are rare, but also because they are difficult to diagnose in the field and are underrepresented in collections. That this specimen went unrecognized for 9 years after being collected underscores the field and museum identification problems posed by hybrids. Hybrids have been reported between Red Kite (*Milvus milvus*) and Black Kite (*M. migrans*) in Sweden (Sylvén 1977), a possible hybrid Rueppell's Vulture (*Gyps rueppellii*) and Cape Vulture (*G. coprotheres*) in Botswana (Borello 2001), Brown Goshawk (*Accipiter fasciatus*) and Grey Goshawk (*A. novaehollandiae*) in Australia (Olsen 1995), Shikra (*A. badius*) and Levant Sparrowhawk (*A. brevipes*) in Israel (Yosef et al. 2001), Pallid Harrier (*Circus macrourus*) and Montagu's Harrier (*C. pygargus*) in Finland (Forsman 1995), Western Marsh Harrier (*C. aeruginosus*) and Eastern Marsh Harrier (*C. spilonotus*) in Siberia (Fefelov 2001), and Greater Spotted Eagle (*Aquila clanga*) and Lesser Spotted Eagle (*A. pomarina*) in Latvia (Bergmanis et al. 1996). We were unable to locate a copy of Suchelet (1897), who apparently reported a hybrid between Common Buzzard and Rough-legged Hawk. Most unusual were intergeneric hybrids reported between Black Kite and Common Buzzard near Rome, Italy, that produced rather strange-looking offspring (Corso and Glidi 1998). Equally unusual was a pairing between Gyrfalcon (*Falco rusticolus*) and Peregrine Falcon (*F. peregrinus*), in which both members of the pair were females (Gjershaug et al. 1998). The hybrid Turkey Vulture × Black Vulture reported by McIlhenny (1937) was later determined to be a practical joke (Jackson 1988). Most instances of hybridization listed above were determined at the nests by observing that the adults were different species, although one was a hybrid captured for banding (Yosef et al. 2001) and another was identified using field observations and photographs (Corso and Glidi 1998).

To our knowledge, our report is the first of a hybrid specimen arising from two *Buteo* species, and, perhaps, the first hybrid specimen for any raptor. It provides the first conclusive documentation of hybridization between two native North American members of the genus *Buteo*. A pairing of a Red-shouldered Hawk with a Gray Hawk (Lasley 1989) produced a downy chick, but it did not fledge, and there were neither photographs nor specimens from this union.

ACKNOWLEDGMENTS

This study was facilitated by the Collections of Birds and the Collection of Genetic Resources at the LSU Museum of Natural Science, and the Collection of Birds at the Museum of Vertebrate Zoology, University of California, Berkeley. We thank S. W. Cardiff and D. L. Dittmann for finding and collecting this unusual specimen and P. Bloom, A. Hinde, Braddock Bay Raptor Research, and Cape May Raptor Banding Project for sharing measurements of juvenile male Swainson's, Rough-legged, and Red-tailed hawks with us. F. K. Barker provided previously unpublished primers for the MUSK gene. J. V. Remsen, Jr., J. Schmutz, T. Swem, S. M. Witt, and an anonymous reviewer made helpful comments on previous drafts.

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The Wilson Journal of Ornithology 118(1):53–58, 2006

NOCTURNAL HUNTING BY PEREGRINE FALCONS AT THE EMPIRE STATE BUILDING, NEW YORK CITY

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ABSTRACT.—We report on nocturnal hunting by Peregrine Falcons (*Falco peregrinus*) at the Empire State Building in Manhattan, New York City. From 4 August through 13 November 2004, we saw Peregrine Falcons on 41 of 77 nights of observation. During this period, they hunted migrating birds on 25 evenings, with the first hunting attempt occurring an average of 119 min after sunset. Peregrine Falcons made 111 hunting attempts and captured 37 birds (33% success). Hunting success was highest in September, but was most often observed in October. Peregrines hunted migratory birds at night more frequently in autumn than in spring. Peregrines were significantly more likely to be present on autumn nights when >50 migrants were passing by the Empire State Building. Although the lights associated with skyscrapers are believed to disorient migrating birds and result in many bird-to-skyscraper collisions each year, Peregrine Falcons are able to take advantage of the situation. Skyscrapers provide hunting perches at altitudes often flown by nocturnal migrants, and disorientation caused by the lights sometimes results in birds circling skyscrapers and possibly becoming more vulnerable to predation by falcons. *Received 26 January 2005, accepted 11 October 2005.*

Several diurnal raptor species, including Black-shouldered Kite (*Elanus axillaris*), Bald Eagle (*Haliaeetus leucocephalus*), and Lesser Kestrel (*Falco naumanni*), forage at night (see Kaiser 1989, McLaughlin 1989, Negro et al. 2000). Others, such as Turkey Vulture (*Cathartes aura*), Osprey (*Pandion haliaetus*), Northern Harrier (*Circus cyaneus*), and Levant Sparrowhawk (*Accipiter brevipes*), have been observed flying or migrating at night (Tabor and McAllister 1988, Russell 1991, Yosef 2003, DeCandido et al. 2006).

Peregrine Falcons (*Falco peregrinus*) are considered nocturnal migrants in some parts of the world (Cochran 1985, Ellis et al. 1990), and they are known to hunt at night (Clunie 1976, Russell 1998). With increased numbers of peregrines nesting and wintering in cities, biologists are beginning to document nocturnal activity by these falcons in all seasons. Recently, there have been reports of urban peregrines feeding young and/or hunting at night in North America (Cade and Bird 1990, Wendt et al. 1991, Cade et al. 1996), England (Crick et al. 2003), France (Marconot 2003), Germany (Schneider and Wilden 1994, Kladny 2001), Netherlands (van Dijk 2000, van Geneijgen 2000), Poland (Rejt 2000, 2001, 2004a), Hong Kong (Feare et al. 1995), and Taiwan (K. Y. Huang and L. L. Severinghaus unpubl. data). However, direct observation and analysis of nocturnal hunting by Peregrine Falcons, particularly during migration, is rare in the literature.

In New York City, New York, the number and distribution of Peregrine Falcons has changed considerably since such observations were first recorded in the late 1920s. Before the era of DDT (until 1946), from autumn through early spring, lone female peregrines were much more common at skyscrapers than males (Herbert and Herbert 1965). Peregrine Falcons rarely nested in the city, and nocturnal activity by these falcons was not reported in any season (Herbert and Herbert 1965). Beginning in the mid-1990s, however, more pairs of Peregrine Falcons have begun residing year-round in Manhattan (and the metropolitan area) than previously noted (B. A. Loucks pers. comm., C. Nadareski unpubl. data.). Today, most, if not all, of the seven pairs of peregrines that nest in Manhattan remain on territory year-round. Here, we report our observations of Peregrine Falcon activity at night during the 2004 southbound bird migration at one location in New York City.

METHODS

Most of our observations of Peregrine Falcons and nocturnal migrants occurred during

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the southbound migration, from 4 August to 13 November 2004; we made observations on 77 of 102 evenings during that period. In spring 2004, we observed northbound migrants on 33 evenings from 19 April through 25 May. In spring 2002, we made observations on only 2 evenings (8 May and 15 May).

We made our observations from the outside observation deck (elevation ~325 m above ground level) of the Empire State Building (ESB), located in midtown Manhattan in New York City. We arrived each evening approximately 15–30 min prior to sunset. Bird migration, on average, began 30–90 min after sunset. Any Peregrine Falcon activities defined as nocturnal occurred after nautical twilight (1 hr after sunset). We were able to conduct our study until 22:45 EST each evening (August through October) and until 23:45 in November; the observation deck of the building was closed to all visitors after these times. In spring 2004, we observed from just before sunset until 22:45 each evening, and in spring 2002, we observed from 19:00 until 21:00. During fall migration, the northwest corner of the building provided the best vantage point to count the greatest number of migrating birds, and in spring, we observed migrants from the southwest corner of the observation deck. These locations afforded unobstructed views to the horizon and the sky above. We used 10× binoculars to follow peregrines when they made long flights in pursuit of prey. It was possible to observe migrating birds and the activities of peregrines because the upper floors of the building were illuminated with (external) upward-directed halogen lights, and the spire above us was illuminated with (internal) florescent lights. We could not identify the majority of migrants to species because the external halogen lights washed out most plumage details. However, this lighting array permitted us to count migrants up to ~30–60 m above the highest point (445 m agl) of the ESB, and up to 30 m (perpendicular) from the observation deck. We estimated that the building's lights allowed us to see peregrines chasing small birds in flight up to 60–80 m distant.

Count protocols to assess nocturnal bird migration in 2004 followed those described in Bildstein and Zalles (1995) for migrating raptors. An individual was considered a migrant if it passed south-to-north (or north-to-south) across an imaginary east-west line at the site, and continued north (or south) out of sight. On 2 evenings during southbound migration, when >100 birds simultaneously circled the ESB, we estimated the maximum number of birds circling per hour and recorded it as the number of migrants seen for that hour. We defined the peak of migration as the several-day period in which we counted the highest number of migrants. For both northbound and southbound migration, total counts presented here do not include migrating waterfowl, herons, or gulls.

We defined a hunting attempt as one in which a Peregrine Falcon approached to within 1 m of its intended prey. On a few occasions, peregrines made repeated stoops at the same prey, but did not capture or gain control of it. Each of these stoops was considered a separate hunting attempt. Several times, we observed a peregrine strike a bird but fail to seize it. We classified these as unsuccessful hunting attempts.

We defined the peak period of Peregrine Falcon activity as that during which we observed falcons at the ESB during the greatest number of consecutive nights. We used correlation statistics (Microsoft Excel 2003) to analyze data collected during this peak period. We compared (a) the time of arrival of the first migrant after sunset with the arrival of the first Peregrine Falcon, and (b) the time of arrival of the first migrant with the time of the first peregrine hunting attempt. Means are presented as ± SD.

RESULTS

During southbound migration in 2004, we saw the first Peregrine Falcon at night on 4 August and the last one on the evening of 9 November. During this time, at least two adult peregrines (male and female), as well as immature(s), used the ESB as a hunting perch. Peregrines were seen hunting or flying at night on 53% (41 of 77) of the evenings we spent at the ESB (Table 1). Falcons were significantly more likely to be present on evenings when >50 migrants were counted in migration (χ^2 = 14.7, df = 1, P = 0.001; Table 1). Of the 67 nights we observed migrating birds, peregrines hunted migrants on 25 nights (37%), made 111 hunting attempts, and cap-

TABLE 1. Summary of nocturnal hunting behavior by Peregrine Falcons in relation to the number of migrants present after sunset in autumn 2004 at the Empire State Building, New York.

	Number classes of migrant passerines						
	0	1–10	11–50	51–100	101–250	251+	Total
No. nights migrants counted	10	9	23	10	13	12	77
No. nights peregrines present	1	1	12	8	9	10	41
No. nights peregrines hunted	—	0	8	3	7	7	25
No. hunting attempts	—	0	29	17	15	50	111
No. successful hunts	—	0	8	7	8	14	37
Hunting success	—	—	28%	41%	53%	28%	33%
No. nights male observed hunting	—	0	5	2	5	6	18
No. nights female observed hunting	—	0	2	1	1	1	5
No. nights unknown sex observed hunting	—	0	1	0	1	1	3

tured prey 37 times (33% success). All of the migrants we observed being captured or chased were in the warbler-to-oriole size class.

The peak of Peregrine Falcon activity occurred from 26 September through 14 October 2004. During that time, we conducted observations on 17 nights; on 16 of those nights we observed Peregrine Falcons, and on 11 nights we observed them hunting (70 total hunts, 21 prey captures, 30% success). During this period, the first migrant birds were observed 65 ± 20 min after sunset (range = 42–114 min); Peregrine Falcons arrived 91 ± 41 min after sunset (range = 47–190 min), and made their first hunting attempt 45 ± 59 min later (range = 61–284 min), or approximately 136 min after sunset. There was no correlation between passage of the evening's first migrant and the arrival of a Peregrine Falcon at the ESB ($r^2 = 0.10$, $P = 0.73$) or between passage of the first migrant and the time of a peregrine's first hunting attempt ($r^2 = 0.15$, $P = 0.24$).

Nocturnal hunting success was greatest in September (12 of 27, 44%) and lowest in November (1 of 8, 13%; Table 2). On 10 October from 20:12 to 20:42, a male Peregrine Falcon made 25 hunting attempts and captured 9 birds (36%), caching the birds on the ESB tower after each kill. Throughout the autumn, we observed Peregrine Falcons capture only migratory birds, although a few Rock Pigeons (*Columba livia*), and at least two bat species, Little Brown (*Myotis lucifugus*) and Red (*Lasiurus borealis*) bats, were present on some evenings. We could identify only two prey species: a Baltimore Oriole (*Icterus galbula*) captured on 23 August, and a Yellow-billed Cuckoo (*Coccyzus americanus*) taken on 9 October. On 3 and 9 November, despite high numbers of American Woodcocks (*Scolopax minor*) migrating past the ESB tower (36 counted each night), no peregrines were observed.

In autumn 2004, most bird migration occurred at eye-level and above the observation deck. We counted 10,826 migrating birds, and the peak of the migration occurred from 5 to 11 October when 3,871 migrants (36% of the

TABLE 2. Summary of nocturnal hunting behavior and success by Peregrine Falcons during four autumn months in 2004 at the Empire State Building, New York.

	Aug	Sep	Oct	Nov	Total
No. hunting attempts	16	27	60	8	111
No. successful hunts	6	12	18	1	37
Hunting success	38%	44%	30%	13%	33%
No. nights one peregrine present	10	11	10	3	34
No. nights ≥2 peregrines present	0	3	4	0	7
No. nights hunting observed	5	9	10	1	25
No. nights male made a hunting attempt	5	7	5	1	18
No. nights female made a hunting attempt	0	2	3	0	5
No. nights unknown sex made a hunting attempt	—	1	2	—	3

fall flight) were counted, averaging 114 birds/hr on these 7 evenings. In spring 2004, we counted 3,359 migrants during 33 nights of observation. The peak of the migration occurred from 6 to 15 May when 1,752 migrants (52% of the spring flight) were counted, averaging 51 birds/hr on these 10 evenings. Lone Peregrine Falcons were observed on 2 evenings: 24 April (0 migrants counted) and 22 May (79 counted), but no hunting attempts were observed on either night. On 15 May 2002, we observed an adult female peregrine make 10 unsuccessful hunting attempts on migrants from 20:15 until 21:00.

In the breeding season of 2004, a pair of Peregrine Falcons may have attempted to nest on the ESB (B. A. Loucks pers. comm.). It is possible that this pair executed many of the hunting attempts we observed in autumn 2004. During 5 evenings between 26 September and 7 October, we saw an adult male and an adult female peregrine perched near one another, each vocalizing with the "eechup" or "creaking" call, and the "wailing" calls (see Ratcliffe 1980). On 3 October, we observed three adults (a male, his mate, and a second female) perched for <5 min within ~20 m of one another on the ESB tower until the second female was chased away—mostly by the female of the pair. An immature peregrine was present on 3 evenings: 9 and 14 October, and 9 November 2004, although we could not be sure if it was the same bird on all 3 evenings. On 5 October, a Peregrine Falcon passed high overhead flying south on moderate northerly winds while an adult female flew back and forth near the ESB. It was not uncommon to see peregrines flying high above (25–75 m) the top of the ESB tower at night in September and October.

DISCUSSION

Tall, lighted, man-made structures present opportunities for biologists to study nocturnal hunting by Peregrine Falcons that may not be observed readily in remote locations. Urban skyscrapers provide hunting platforms that permit these raptors to perch at or above the elevation of nocturnal migrants, and the lights used to illuminate tall buildings can disorient migrating birds that may then circle these structures, especially on evenings with overcast skies and light winds. These migrants constitute an abundant, easily accessible resource for resident Peregrine Falcons, and for peregrines migrating through the area as well.

In New York City in 2004, Peregrine Falcons were more likely to be present and hunting at the ESB on autumn nights when >50 migrants were observed. The peak of peregrine activity at the ESB corresponded to the peak of the southbound bird migration from late September through mid-October. During this time, two adult peregrines occasionally perched near one another and used the ESB as a hunting platform. More night migrants were attracted to the building's lights during autumn rather than spring migration, and many more circled the tower for longer time periods from August through late October. In spring, there are fewer nocturnal migrants, and these mostly pass higher above New York City on warm air currents that override heavier, cooler air near the ground (see Kerlinger and Moore 1989). Each of these factors likely influences a peregrine's decision to hunt migrants more frequently at night during autumn. On the only spring night (15 May 2002) during which we did see several peregrine hunting attempts, winds were ~24–32 km/hr from the northwest, and many migrants passed at or just above the level of the observation deck.

Peregrine Falcons hunted migrants in two ways: pursuit and "still hunting" (*sensu* Cade 1982). At the ESB, greater success occurred when they pursued prey in level flight from behind; however, peregrines more often employed still hunting from a west- or north-facing perch on the spire above the observation deck. When still hunting, they launched their attacks at a 5 to 15° angle down toward incoming migrants flying along a northwest-to-southwest route past the ESB. Such direct attacks were often unsuccessful, and peregrines had to make additional short stoops to secure the prey. If the intended prey was able to dodge the initial attack, it would then fly straight down toward the ground, and peregrines often made no further pursuits. We never observed targeted prey attempt to escape by "ringing up," nor did we ever observe birds mass together in a flock when a Peregrine Falcon flew among them. On some nights (e.g., 10 October), when many migrants passed the ESB and peregrines captured several birds, we also observed unsuccessful hunting attempts that were considerably less intense than others made on the same evening. Such behavior may account for the low hunting success rate on nights when >250 migrants were counted.

As camera use increases for 24-hr nest surveillance, it may become possible to determine whether Peregrine Falcons frequently hunt at night during the nesting season, and whether this varies from year to year (see Rejt 2004b). Future studies at the ESB may also determine whether nocturnal flights made toward conspecifics are directed at neighboring Peregrine Falcons or at night-migrating falcons simply passing through the area.

ACKNOWLEDGMENTS

We thank B. A. Loucks for information and kind words of encouragement. We also acknowledge C. A. Nadareski's long-term work with Peregrine Falcons in the metropolitan area. A. Bräunlich and E. J. A. Drewitt directed us to recent literature about nocturnal Peregrine Falcon activity in Europe and Asia. We thank H. Q. P. Crick for providing information about Peregrine Falcons in England. K. L. Bildstein, J. B. Buchanan, and D. Panko each critically read the manuscript and made many helpful suggestions regarding how to interpret the data. We also wish to thank two anonymous reviewers for their comments and ideas. In New York City, S. Critelli, C. R. Howard, M. W. Kolakowski, W. J. Paulson, B. J. Saunders, E. Shapiro, S. J. Wiley, and C. A. Wood observed Peregrine Falcons with us. We thank the staff of the Empire State Building, including L. A. Ruth and all security personnel, for facilitating our research and making our evenings at the building much more pleasant. We dedicate this paper to Rev. M. A. Hegyi who encouraged the senior author to study New York City's fauna and flora. This is Hawk Mountain Sanctuary's contribution to conservation science number 124.

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The Wilson Journal of Ornithology 118(1):59–63, 2006

FIELD EXPERIMENTS ON EGGSHELL REMOVAL BY MOUNTAIN PLOVERS

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ABSTRACT.—I conducted 18 eggshell removal trials at six Mountain Plover (*Charadrius montanus*) nests in the Pawnee National Grassland, Weld County, Colorado, during June 1994. Eggshell fragments were placed at various distances (10 cm to 10 m) from active nests. Attending adult plovers removed eggshells throughout the incubation period. When eggshells were placed within 2 m of the nest, plovers usually removed them immediately upon their return to the nest. Shells placed farther away—up to 10 m—were removed after longer time intervals. Plovers removed shells by picking them up with their bills and running or flying away with them before dropping them 6 to 100 m from the nest. When returning to their nests, plovers approached by ground. Of the five hypotheses proposed in the literature to explain the function of eggshell removal behavior in birds, only one (reducing cues predators might use for finding nests) predicts removal of shells already outside the nest and disposal of shells far from the nest. Thus, my results support an anti-predator function for eggshell removal in Mountain Plovers. *Received 3 November 2004, accepted 1 October 2005.*

Shortly after their young hatch, many birds remove the empty eggshells and dispose of them away from the nest (Nethersole-Thompson and Nethersole-Thompson 1942, Skutch 1976). This behavior is well developed in charadriiform birds, including shorebirds and gulls. In their classic paper, Tinbergen et al. (1962) suggested five possible hypotheses for the adaptive value of eggshell removal behavior: (1) eggshells might provide cues that would attract predators to the nest; (2) later-hatching eggs might become encapsulated, the young in hatching eggs thus becoming trapped inside a double shell (termed "egg-capping" by Derrickson and Warkentin 1991); (3) sharp edges of shells might injure chicks in the nest; (4) organic material associated with eggshells might promote growth of pathogenic bacteria and mold in the nest; and (5) hatched shells could interfere with brooding chicks in the nest. Tinbergen's field experiments with gull eggs, which are cryptically colored externally but conspicuously white inside, supported the first hypothesis by showing that artificial nests with eggshells nearby experienced greater predation rates than those without nearby eggshells (Tinbergen et al. 1962, Tinbergen 1963). Tinbergen, however, did not rule out the remaining hypotheses. Subsequent literature has tended to support the predation (Sordahl 1994, Sandercock 1996) and egg-capping hypotheses (Derrickson and Warkentin 1991, Sandercock 1996, Verbeek 1996, Hauber 2003).

Hypotheses 3, 4, and 5 seem unlikely explanations of the evolution of eggshell removal behavior in shorebirds because their eggs usually hatch synchronously and the precocial young leave the nest within 24 hr of hatching. Sandercock (1996) reported observations of egg-capping in two sandpiper species, supporting hypothesis 2. However, he recognized that egg-capping alone could not account for the form of removal behavior typically seen in shorebirds—specifically, the disposal of eggshells far from the nest—and concluded that both egg-capping and predation have contributed to the evolution of eggshell removal behavior in these birds.

Here, I report the results of field trials on eggshell removal behavior of Mountain Plovers (*Charadrius montanus*). Mountain Plovers nest on the ground in very open habitat, where predation is the major cause of egg and chick losses (Graul 1975, McCaffery et al. 1984, Sordahl 1991, Miller and Knopf 1993, Knopf 1996, Knopf and Rupert 1996). General aspects of eggshell removal in this species were described by Graul (1975). My experiments enabled me to provide a quantitative description of the behavior and to evaluate its function.

METHODS

I performed field trials on eggshell removal by Mountain Plovers from 9 to 18 June 1994 at Pawnee National Grassland, Weld County,

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TABLE 1. Results of 18 field trials on eggshell removal behavior at six Mountain Plover nests, Pawnee National Grassland, Colorado, 9–18 June 1994. In each trial, one-third of a complete eggshell (of Mountain Plover or Japanese Quail) was placed near the nest and the behavior of the adult was observed upon its return to the nest.

Nest[a]	Incubation day	Shell type	Nest–shell distance (m)	Time until removal (min)	Removal method	Disposal distance (m)
S1	5	Quail	0.5	0.08	Fly	70
S1	6	Quail	0.7	10	—[b]	—
S1	7	Quail	0.6	0	Fly	60
K1	7	Quail	1.0	0	Run-fly	30
K1	8	Quail	0.5	0.17	Run	6
K1	8	Quail	2.5	97	Run	17
K1	8	Quail	5.0	105	—	—
K1	8	Quail	10.0	—	—	22
K1	9	Quail	1.5	26	—	—
S2[c]	8	Quail	0.2	0	Run	20
S2	8	Quail	0.5	0	Run	30
K2	15	Plover	2.0	3	Run-fly	100
K2	16	Quail	3.0	0	Run	18
K2	16	Quail	4.0	69	—	—
R1	20	Plover	0.1	0	Run	12
R1	23	Plover	0.3	0	Fly	90
R1	25	Quail	0.7	0	Run	15
K3	27	Plover	1.5	0	Run	18

[a] Mountain Plovers typically exhibit uniparental care; therefore, egg removals were assumed to represent the behavior of one adult per nest.

[b] Missing data in the table indicate that shell removal was not observed (see text) or that the disposed shell was not found.

[c] Nest S2 contained four eggs; all other nests contained three.

Colorado (40° 45′ N, 104° 00′ W). This shortgrass prairie site has been well described elsewhere (Graul 1973, 1975; McCaffery et al. 1984). Its vegetation was very short and sparse, and it was grazed by cattle.

I studied eggshell removal at six Mountain Plover nests. Five nests contained three-egg clutches (normal for Mountain Plovers) and one nest contained four eggs. The attending adults were not marked for identification, but since uniparental care is typical in this species (Knopf 1996), it is likely that I tested six different individuals. Mountain Plovers are sexually monomorphic (Hayman et al. 1986, Knopf 1996), so I was unable to determine the sex of the birds. Trials entailed placing approximately one-third of a complete eggshell on the ground (interior—or white—side up) at various distances (ranging from 10 cm to 10 m) from the nest and then observing the behavior of the adult when it returned to its nest. I conducted 18 trials, 14 with Japanese Quail (*Coturnix japonica*) eggshells obtained commercially and 4 with Mountain Plover eggshells that I found opportunistically in the field. The two species' shells are similar in size and appearance, both having earth-tone background colors and dark, irregular markings. Adult plovers responded similarly to the two kinds of shells; therefore, I pooled the results.

Observations were made from a vehicle about 100 m from nests with 7 × 35 binoculars. For each trial, I recorded the nest-to-shell distance, the amount of time elapsed between the adult's return to the nest and removal of the shell, the removal method (run or fly), the disposal distance, and the method (run or fly) of returning to the nest after shell disposal. At least one egg hatched in every nest and, assuming that incubation begins when the clutch is complete and the average incubation period is 29 days (Knopf 1996), I used backdating to determine days since incubation began. I measured the distances of eggshells from nests with a tape measure, and disposal distances of shells that I was able to relocate by pacing.

RESULTS

The number of trials conducted at each of the six nests was 6, 3, 3, 3, 2, and 1 (Table 1). The attending adult Mountain Plover removed shells at all six nests. Nine of 18 shells

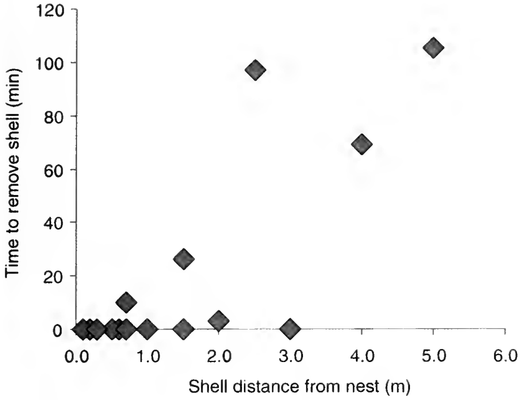

FIG. 1. Relationship between the distance eggshells were placed from Mountain Plover nests and the time elapsed before the adult removed the shell, 9–18 June 1994, Pawnee National Grassland, Weld County, Colorado. Three of the 17 points overlap at 0.5 m (2 are hidden).

were removed immediately upon the adult's return to the nest; 2 more were removed within 10 sec. Two other shells were removed 3 min and 10 min after the adults had returned. Four of the remaining five shells were removed in less than 2 hr. The final shell, placed 10 m from the nest, was not removed during 15 min of observation, at which time I departed the nest site; the following morning I found the shell 22 m from the nest. Although it is possible that the wind or another animal moved this shell, it seems most likely that the adult plover moved it. Overall, shells placed within 2 m of the nest were removed promptly (most of them immediately), whereas shells placed farther away were removed after longer intervals (Fig. 1). Eggshell removal was documented on incubation days 5–9, 15, 16, 20, 23, 25, and 27 (Table 1).

I recorded eggshell removal and adult return to the nest for 13 of 18 trials (Table 1). During the remaining five trials, which had long eggshell removal times, my vigilance was intermittent and I did not observe the actual removal. However, by checking for the eggshell as soon as I noticed that the bird was off the nest, I was able to record removal times with only a small margin of error (except in the case described above, where I left the site before removal occurred). When a Mountain Plover removed an eggshell, it picked the shell up with its bill and ran away with it (8 of 13 observations), flew off with it (3 of 13 observations), or ran 2–3 m before flying off with it (2 of 13 observations). On 14 occasions I was able to recover shells where they were dropped; disposal distances ranged from 6 to 100 m from the nest (Table 1). Plovers tended to dispose of shells at greater distances when they flew (mean = 70.0 m, range = 30–100, n = 5) than when they ran (mean = 17.0 m, range = 6–30, n = 8). On four occasions I recorded which facet (inside or outside) of a recovered shell was exposed; two shells were lying with the cryptic outside facing up and two were lying with the conspicuous inside of the shell facing upward. After disposing of the shells, adults always returned to their nests by a ground approach (13 of 13 observations), which is typical of plovers (TAS pers. obs.).

DISCUSSION

My field experiments demonstrated that Mountain Plovers remove eggshells throughout the incubation period. This may be true for most birds, and the expression of the behavior long before hatching occurs likely has been selected for in the context of removal of damaged eggs (Nethersole-Thompson and Nethersole-Thompson 1942, Montevecchi 1976, Kemal and Rothstein 1988, Sordahl 1994). Removal of dead chicks from the nest also has been reported (Nethersole-Thompson 1951:183, Skutch 1976:284, Sordahl 1994).

Because it had already been demonstrated that Mountain Plovers remove eggshells located *in* their nests (Graul 1975, Knopf 1996; TAS pers. obs.), I designed my experiments to determine whether they would remove shells placed outside the nest and, if so, how far from the nest they would go to remove shells. I observed adults immediately remove shells that had been placed up to 3 m from their nests (Table 1, Fig. 1). They also eventually removed shells at distances of 4, 5, and probably 10 m, as well. Because the average disposal distance was only 17 m for birds that removed eggshells by running, it seems unlikely that Mountain Plovers would remove shells located much farther from their nests than 10 m.

The closer a shell was placed to the nest, the more quickly it was removed (Fig. 1). The proximate explanation for this probably is that adults were less likely to detect eggshells that were farther from the nest. Even though Mountain Plover nesting habitat is shortgrass prairie, the line of sight a plover has when making a ground approach to its nest is low enough that even small obstructions could interfere with its ability to notice a distant shell. An ultimate explanation for this finding would be that the risk of predation due to the presence of eggshells diminishes with distance from the nest, as shown by Tinbergen et al. (1962) for Black-headed Gull (*Larus ridibundus*) eggs. Tinbergen et al. (1962) found that a broken eggshell ≤1 m from an artificial clutch increased the predation rate, but an eggshell 2 m away did not. If the radius of increased risk is similar for Mountain Plovers, one might expect them to be less diligent about removing shells >2 m from the nest. My results are consistent with this because the birds did not immediately remove shells that were >2–3 m away. Nevertheless, they eventually did remove those shells, which suggests that such shells pose at least some risk to the clutch.

Although eggshell removal and disposal distances have not been investigated systematically in birds, these distances most likely represent a compromise between the benefits of removal and the costs of leaving the nest when young are hatching. Factors that probably influence these distances are habitat (especially open habitats in the case of Mountain Plovers), the degree of nest dispersion (widely spaced in Mountain Plovers), and which species of egg and chick predators inhabit the area (mammals and snakes are thought to be important predators of Mountain Plovers; Knopf 1996).

Of the five hypotheses explaining the adaptive value of eggshell removal, the only one that predicts removal of eggshells already outside the nest is the predation hypothesis. It also is the only hypothesis that predicts disposal far from the nest. Thus my results support an anti-predator function for eggshell removal in Mountain Plovers. Similarly, fecal sac removal by many nidicolous birds (which is analogous to eggshell removal) involves disposal of fecal sacs far from the nest (Petit et al. 1989 and references therein), and this behavior also seems best explained as a means of reducing cues that could lead predators to nests (Petit et al. 1989, Lang et al. 2002). However, I cannot rule out the possibility that eggshell removal serves functions other than predation avoidance. For example, if there is a risk that wind may blow shells back into the nest, it may be adaptive to dispose of them far away so they do not threaten the chicks with encapsulation or injury. Further research is needed to examine these alternative explanations of eggshell removal behavior.

ACKNOWLEDGMENTS

I especially thank C. A. Ristau for enabling me to study Mountain Plovers in Colorado. She and F. L. Knopf generously shared information about nests they had found. The manuscript benefited from comments by D. I. Bishop, S. J. Dinsmore, M. B. Wunder, and two anonymous referees. This research was conducted, in part, on the Central Plains Experimental Range operated by the USDA Agricultural Research Service and made available to the Long Term Ecological Research Program administered by Colorado State University. I thank M. Lindquist for courtesies extended during my stay. I was supported by a Luther College Faculty Research Grant.

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The Wilson Journal of Ornithology 118(1):64–69, 2006

SEED-SIZE SELECTION IN MOURNING DOVES AND EURASIAN COLLARED-DOVES

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ABSTRACT.—I studied seed-size selection among Mourning Doves (*Zenaida macroura*) and Eurasian Collared-Doves (*Streptopelia decaocto*), two newly sympatric species for which mechanisms of seed selection are not well understood. I measured and compared mean length, breadth, and thickness of seeds available to, and consumed by, these species in feeding trials of penned birds. Both species selected corn (*Zea mays*) seeds that were shorter and narrower than average, but Eurasian Collared-Doves selected corn that was thicker than average and sunflower (*Helianthus annuus*) seeds that were broader and thicker than average. Mourning Doves consumed corn of average thickness, and wheat (*Triticum aestivum*) and sunflower seeds of average size with respect to all dimensions. Corn consumption by both species seems limited by seed length and breadth, but Mourning Dove consumption of smaller seed types (wheat and milo [*Sorghum vulgare*]) appears largely unaffected by seed size. Among larger seed types (corn and sunflower), Eurasian Collared-Doves may select thicker- and/or broader-than-average seeds to maximize foraging efficiency. Sunflower and corn seeds consumed did not vary between species with respect to any dimension, but Eurasian Collared-Doves seemed willing to select, and able to eat, broader and thicker seeds than Mourning Doves, which may limit foraging competition between these species. *Received 7 February 2005, accepted 23 November 2005.*

Seed selection by granivorous birds is a complex phenomenon potentially affected by a number of factors (Ramos 1996), the relative contributions of which remain poorly understood in many avian granivores. In particular, seed selection by doves and other species that do not husk seeds before swallowing is not well understood; most studies of seed selection in birds have focused on finches and other species that husk seeds during the course of foraging. Generally, these studies have revealed that the physical characteristics of seeds affecting handling time, such as size, shape, and hardness, are important determinants of preference, and that nutritional composition of foods appears relatively unimportant (Willson 1971, Willson and Harmeson 1973, Goldstein and Baker 1984, De Nagy Koves Hrabar and Perrin 2002), especially without consideration of the overall economics of nutrient intake and the factors affecting it (Greig-Smith and Wilson 1985).

One approach to understanding the effect of seed size on selection has been to examine size selection by one or more species for a single seed type (Hespenheide 1966, Myton and Ficken 1967, Willson 1972, Abbott et al. 1975, Greig-Smith and Crocker 1986, van der Meij and Bout 2000). A number of these studies have indicated seed-size preference within a species (Greig-Smith and Crocker 1986, van der Meij and Bout 2000), and/or correspondence between size selection and bill size among multiple species (Hespenheide 1966, Myton and Ficken 1967, Willson 1972). One study indicated no size preferences and/or no seed size/bill size correspondence (Abbott et al. 1975), but this study focused on a seed-husking species. Because doves and pigeons have relatively long slender bills and pecking behaviors that maximize speed of seed intake without husking seeds (De Nagy Koves Hrabar and Perrin 2002), seed size may be expected to affect seed handling and preferences differently than in most species studied previously.

The overall goal of this project was to determine the effect of seed size on food selection by Mourning Doves (*Zenaida macroura*) and Eurasian Collared-Doves (*Streptopelia decaocto*). Eurasian Collared-Doves are recent exotic invaders of North America, and may compete for food or other resources with native species, such as Mourning Doves, to the detriment of native species (Romagosa 2002). Bill-size-related differences in seed-size selection between Eurasian Collared-Doves and Mourning Doves may mitigate competition between these species for food resources, however (Poling and Hayslette 2006). Subdivision of food resources among sympatric avian granivores often is based on bill-size-relat-

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ed differences in seed-size selection (Grant 1986, Faaborg 1988, Ricklefs 2001). Mourning Dove bill length averages 12.83–14.53 ± 0.97–1.01 mm (Mirarchi and Baskett 1994), whereas collared-dove bill length averages 16.9 ± 0.71 mm for males and 16.6 ± 1.02 mm for females (Romagosa 2002). Corresponding differences in seed-size selection patterns between these species may have important implications regarding dietary overlap and competition, and ultimately, coexistence of the two species.

In cafeteria trials, previous work has indicated that Mourning Doves and other dove species prefer small, round seeds such as white proso millet (*Panicum miliaceum*; Hayslette and Mirarchi 2001, De Nagy Koves Hrabar and Perrin 2002), and consume relatively few large-seeded species such as corn (*Zea mays*) and sunflower (*Helianthus annuus*; LeBlanc and Otis 1998, Hayslette and Mirarchi 2001). These results appear enigmatic, as wild Mourning Doves are known to exploit corn and sunflower as important food sources (Lewis 1993). De Nagy Koves Hrabar and Perrin (2002) concluded that among Diamond Doves (*Geopelia cuneata*), seed size becomes a limiting factor above a threshold size, but below that threshold, size is of little importance in food handling and selection. I hypothesized that seed size has little influence on Mourning Dove selection of small seeds, but that preferences for, and consumption of, larger seeds, such as corn and sunflower, are limited by seed size. Based on this hypothesis, I predicted that Mourning Doves would preferentially select smaller than average corn seeds, and that this within-seed-type selectivity for size would decrease with progressively smaller seed types. I also hypothesized that Eurasian Collared-Doves are less limited than Mourning Doves by size of corn and sunflower seeds because their bills are larger; thus, they are able to exploit corn and sunflower food sources to a greater extent than Mourning Doves. Previous research has shown that Eurasian Collared-Doves consume more corn than Mourning Doves in cafeteria trials (Poling and Hayslette 2006). Based on this, I predicted that Eurasian Collared-Doves would show less within-seed-type selectivity for smaller corn and sunflower seeds than Mourning Doves, and would select larger corn and sunflower seeds than Mourning Doves.

METHODS

The first phase of this research was conducted at the captive Mourning Dove research facility at Auburn University, Alabama, from June to August 2000. I used 15 2nd-year Mourning Doves, captured as immatures on the university campus during the previous breeding season; doves were initially housed and cared for according to Mirarchi (1993). Prior to feeding trials, doves were fed an equal mixture (by volume) of the four foods used in feeding trials (described below) plus proso millet and browntop millet (*Panicum fasciculatum*). I randomly assigned doves to five flocks of three birds each, and each flock was used in a 20-hr feeding trial in a 3.7 × 7.3 × 2.0-m outdoor aviary. During each trial, doves were offered 200 seeds of each of four species—corn, black-oil sunflower, milo (*Sorghum vulgare*), and wheat (*Triticum aestivum*). Trials were preceded by ≥24-hr acclimation periods, during which doves were fed an equal mixture (by volume) of test seeds only, followed by 24-hr fasting periods. Prior to each trial, I estimated size of seeds offered using a sample of 20 seeds drawn at random from each 200-seed batch. I attempted to insure that sizes of seeds in samples were representative of those in feeding batches by comparing the mass of each sample to the mass of the batch from which it was drawn. Because I sampled 10% of each batch (20 out of 200 seeds), mass of a representative sample would be 10% of the mass of the batch from which it was drawn. Thus, a sample was deemed representative and used if the ratio of sample mass to batch mass was 0.100 ± 0.003. If not, the sample was returned to the batch and redrawn. Using digital calipers, I measured length, breadth, and thickness (corresponding to the longest, intermediate-most, and shortest dimensions, respectively; Greig-Smith and Crocker 1986) of each seed in each sample to the nearest 0.1 mm. Seeds of each species were then hand-scattered on a separate wooden seed tray (41 × 41 × 4 cm) filled with commercially available topsoil; trays were randomly arranged in a 2 × 2 arrangement on the floor of the aviary, with 1.8 m between adjoining trays. After allowing doves to forage from the trays for 20 hr, I removed the trays and removed and counted the seeds that remained on the trays. If ≥20 seeds remained, I estimated size of seeds remaining in the batch using a sample of 20 seeds as before the trial. Analogous to pre-trial sampling, post-trial samples were deemed acceptable based on comparisons of sample mass and batch mass. A sample was used if the ratio of sample mass to batch mass was within 0.003 of the ratio of sample seed number (20) to batch seed number. If not, the sample was returned to the batch and redrawn. I compared number of seeds consumed among seed types using one-way analysis of variance (ANOVA) and Tukey's procedure. I calculated mean size of each pre- and post-trial sample with respect to all three size dimensions. I calculated the average size of seeds consumed with respect to each dimension for each seed type in each trial based on number of seeds consumed and pre- versus post-trial differences in average available seed size. The formula for this calculation is

$$S_e = \{(200 \times S_b) - [(200 - N_e) \times S_a]\}/N_e,$$

where S_e = average size of seeds eaten, S_b = average size of seeds prior to foraging (initial sample), S_a = average size of seeds not consumed, and N_e = number of seeds consumed. I then used a paired *t*-test—with trials as replicates—to compare mean size consumed with mean size available for each size dimension and each seed type.

The second phase of this research was conducted at the captive avian research facility at Tennessee Tech University during January–April 2004. I used 14 Mourning Doves and 13 Eurasian Collared-Doves captured during July–September 2003 in Coffee County, Tennessee. Methods generally followed those used previously, except as noted below. Individuals of each species were tested in a sequential manner in 2.4 × 1.8 × 1.8-m pens. Corn and sunflower seeds (n = 200) were presented to each individual in separate 5.5- and 4-hr trials, respectively; trials involving corn were longer due to the slower consumption of corn by both species. Trial order (i.e., seed type) was determined randomly for each dove, so that approximately half the individuals received corn first, and half received sunflower first. The two trials for each dove were preceded by 24-hr acclimation and fasting periods. Seeds were scattered in trays without topsoil. Pre- and post-trial seed sampling and measurements were conducted as in the previous trials, and similar analyses were conducted separately for each species, with individuals serving as replicates. Additionally, I used two-sample *t*-tests to compare the average length, breadth, and thickness of seeds, by seed type, that each dove species consumed. Trials in which doves consumed <25 seeds were omitted from analyses because I suspected that dove foraging during these trials was too limited to allow for sufficient discrimination among available seeds. I did not conduct statistical comparisons of corn and sunflower consumption because trial length differed between seed types. I conducted all analyses using SAS/STAT (SAS Institute, Inc. 1990) and set α = 0.05. All means are presented ± SE.

RESULTS

In the first phase (2000 Alabama study), consumption of seeds during trials varied among seed types ($F_{3,19}$ = 11.9, $P < 0.001$). Doves consumed more milo, wheat, and sunflower (161.2 ± 24.3, 142.2 ± 20.4, and 103 ± 23.4 seeds, respectively), than corn (8.4 ± 3.0 seeds). Doves ate nearly all (198+) of the 200 milo seeds offered in three of five trials, and consumed almost no (≤2) corn seeds in two of five trials, so these seed types were excluded from further analyses. One trial, in which doves ate 198 wheat seeds, was omitted from analysis of wheat size consumption. Wheat and sunflower seeds consumed were average in size with respect to all dimensions (Table 1).

In the second phase (2004 Tennessee study), Mourning Doves consumed 24.9 ± 4.1 corn and 50.1 ± 10.3 sunflower seeds, and Eurasian Collared-Doves consumed an average of 47.0 ± 4.9 corn and 52.5 ± 8.7 sunflower seeds during trials. Two collared-doves and eight Mourning Doves ate <25 corn seeds, and one collared-dove and four Mourning Doves ate <25 sunflower seeds; these doves were not included in seed-size analyses. Both Mourning Doves and Eurasian Collared-Doves selected smaller-than-average corn seeds with respect to length and breadth (Table 1). Mourning Doves consumed corn seeds

TABLE 1. Measurements (mm) of seeds initially available to, and consumed by, Mourning Doves (MODO; 2000 and 2004) and Eurasian Collared-Doves (EUCD; 2004) in seed-size selection trials on captive birds in Tennessee and Alabama.

					Initially available		Consumed		
Year	Food	Dimension	Species	n^a	Mean	SE	Mean	SE	t^b
2000	Wheat	Length	MODO	4	6.3	0.1	6.4	0.2	−0.9
		Breadth	MODO	4	3.1	0.0	3.1	0.0	0.3
		Thickness	MODO	4	2.6	0.0	2.5	0.0	1.3
	Sunflower	Length	MODO	5	9.8	0.1	10.3	0.5	−1.1
		Breadth	MODO	5	5.2	0.1	5.0	0.2	2.6
		Thickness	MODO	5	3.1	0.1	2.7	0.3	2.0
2004	Corn	Length	MODO	6	12.7	0.1	12.3	0.1	4.3^c
			EUCD	11	12.7	0.1	12.1	0.3	2.7^c
		Breadth	MODO	6	8.4	0.1	7.9	0.2	6.1^c
			EUCD	11	8.4	0.0	7.6	0.2	5.3^c
		Thickness	MODO	6	4.5	0.1	4.6	0.3	−0.3
			EUCD	11	4.6	0.1	5.2	0.2	-3.0^c
	Sunflower	Length	MODO	10	10.4	0.1	10.5	0.3	−0.4
			EUCD	12	10.2	0.1	10.2	0.4	0.2
		Breadth	MODO	10	4.9	0.0	5.0	0.3	−0.1
			EUCD	12	4.9	0.1	5.8	0.3	-3.0^c
		Thickness	MODO	10	2.9	0.0	3.0	0.3	−0.3
			EUCD	12	2.8	0.0	3.5	0.2	-3.5^c

[a] Sample size (n) equals number of three-bird flocks in 2000, individual doves in 2004.
[b] t-values from paired t-tests comparing sizes of seeds initially available and seeds consumed; df = $n - 1$.
[c] $P < 0.05$.

of average thickness, but collared-doves selected corn seeds that were thicker than average. Mean size of corn seeds consumed by the two species did not differ with respect to length, breadth, or thickness ($-1.0 \leq t_{15} \leq 2.8$, all $P \geq 0.11$). Mourning Doves consumed sunflower seeds that were of average size with respect to all dimensions, and average length, breadth, and thickness of sunflower seeds consumed were similar (within 0.3 mm) to average sizes consumed by Mourning Doves in the 2000 study. Eurasian Collared-Doves consumed sunflower seeds of average length, but selected seeds of larger than average breadth and thickness. Mean size of sunflower seeds consumed did not differ ($-0.7 \leq t_{20} \leq 1.6$, all $P \geq 0.12$) between dove species with respect to any dimension.

DISCUSSION

Results suggest that seed length and breadth limit Mourning Dove consumption of corn; seed thickness seems less important in selection. If seeds such as corn are oriented lengthwise as they are swallowed, it seems logical that the smaller of the two cross-sectional dimensions (thickness) would be less important in determining ease with which seeds are swallowed. Thickness seems important, however, in species that husk seeds before swallowing. In a similar study of Eurasian Bullfinches (*Pyrrhula pyrrhula*), sunflower seeds consumed were 4.6% thinner, 3.1% narrower, and 2.1% shorter than average (Greig-Smith and Crocker 1986). Willson (1972) concluded that Purple Finches (*Carpodacus purpureus*) selected seeds based on thickness rather than length. The sunflower seeds we used seemed to be below the size threshold suggested by De Nagy Koves Hrabar and Perrin (2002), above which size becomes a factor affecting dove seed handling and selection. We used seeds of black oil sunflower, a relatively small-seeded sunflower variety commonly used in food plantings for Mourning Doves in the southeastern U.S. These seeds were smaller than sunflower seeds used in previous studies (Hespenheide 1966, Willson 1972, Greig-Smith and Crocker 1986, Diaz 1990). As predicted, consumption of smaller seeds, such as milo and wheat, seemed unaffected by seed size. Preference by Mourning Doves for milo in this study agrees with preference patterns documented elsewhere (Poling and Hayslette

2006), and suggests that seed preference in this species may be based, at least in part, on seed size and/or shape. Selection patterns favoring small seeds have been documented in several studies of seed-husking species (Hespenheide 1966; Willson 1971, 1972; Keating et al. 1992), but De Nagy Koves Hrabar and Perrin (2002) suggested that dove food preferences are influenced more by seed shape than size; round seeds are handled more rapidly than, and preferred to, elongate seeds. Because milo was both the smallest and roundest of the seeds we tested, it is impossible to tell which of these seed characteristics actually influenced seed selection.

As with Mourning Doves, consumption of corn by Eurasian Collared-Doves seems limited by seed length and breadth. In contrast to Mourning Doves, however, Eurasian Collared-Doves were influenced by corn seed thickness, choosing thicker-than-average seeds. If seed thickness is relatively unimportant in determining handling and/or swallowing efficiency, as postulated earlier for Mourning Doves, perhaps the Eurasian Collared-Dove's selection of thicker seeds increases foraging efficiency by increasing nutrient intake (benefit) per unit handling time (cost) (Stephens and Krebs 1986). Likewise, selection of broader- and thicker-than-average sunflower seeds may increase foraging profitability of Eurasian Collared-Doves. Selection for large foods, presumably to maximize foraging profitability, has been reported in other seed-eating birds (Myton and Ficken 1967, Ramos 1996).

Selection of larger than average corn and sunflower seeds with respect to certain dimensions by Eurasian Collared-Doves, but not by Mourning Doves (paired t-tests), suggests that collared-doves select thicker corn seeds, and broader and thicker sunflower seeds, than do Mourning Doves. Although direct between-species comparisons of average seed sizes consumed failed to reveal any such differences, the average corn seed consumed by collared-doves was 0.5 mm thicker than that eaten by Mourning Doves, and the average sunflower seed consumed by collared-doves was 0.8 mm broader and 0.5 mm thicker. Selection for larger seeds by Eurasian Collared-Doves than by Mourning Doves likely is related to differences in their bill sizes (Hespenheide 1966, Myton and Ficken 1967, Willson 1972).

Previous authors have expressed concern about how the recent Eurasian Collared-Dove invasion of North America may affect native species, particularly ecologically similar species, such as the Mourning Dove, with which Eurasian Collared-Doves may compete (Romagosa and McEneaney 1999, Romagosa and Labisky 2000, Romagosa 2002). A recent study of food-selection patterns of these two dove species revealed a high degree (95%) of dietary overlap between them (Poling and Hayslette 2006), although this was based on relative consumption of different seed types in a cafeteria experiment, rather than on size preferences within seed types. If genuine, the Eurasian Collared-Dove's preferences for seeds that are broader and/or thicker than those selected by Mourning Doves may result in differential exploitation of larger seeds, such as corn and sunflower, and concomitant mitigation of foraging competition between them. Partitioning of food resources among sympatric species based on seed size has been documented in a number of avian granivore communities (Grant 1986, Faaborg 1988, Ricklefs 2001). Similarly, limited foraging competition may mean greater potential for coexistence of Mourning Doves and Eurasian Collared-Doves than previously believed.

ACKNOWLEDGMENTS

I thank M. P. Cook, A. Goodman, T. D. Poling, C. Smith, D. Smith, C. Spiller, J. Turner, and T. M. Undeutsch for assistance with data collection. Funding and other support for this project was provided by the Alabama Department of Conservation and Natural Resources (Division of Wildlife and Freshwater Fisheries), Auburn University School of Forestry and Wildlife Sciences, Tennessee Tech University Department of Biology, and Tennessee Wildlife Resources Agency. This research was approved by, and conducted in accordance with, the Auburn University Institutional Animal Care and Use Committee (protocol review number 0009-R-0786), and Tennessee Tech University Institutional Committee for the Care and Use of Lab Animals in Experimentation (protocol review number 1[02–03]). I thank M. R. Perrin and two anonymous referees for their comments on an earlier draft of the manuscript.

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The Wilson Journal of Ornithology 118(1):70–74, 2006

LOW NESTING SUCCESS OF LOGGERHEAD SHRIKES IN AN AGRICULTURAL LANDSCAPE

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ABSTRACT.—Southeastern Illinois is dominated by cropland, and the remaining pastures or grasslands are marginally suitable for breeding Loggerhead Shrikes (*Lanius ludovicianus*), owing, in part, to limited nest sites. From 1998 through 2000, we recorded poor nest success (26%) among shrikes, although results of earlier studies (1967–1972) in this region indicated that nest success was 72 to 80%. Clutch size (5.7 eggs) and fledglings/successful nest (4.4 young/successful nest) were similar to those reported in previous studies. During our study, generalist mammalian predators were abundant, and most nest failures (88%) were caused by predation. We suggest that the loss of grassland habitat and agricultural intensification has resulted in reduced nest success, and this may be true in other areas of the species' range as well. *Received 20 August 2003, accepted 23 November 2005.*

The Loggerhead Shrike (*Lanius ludovicianus*) is of conservation interest throughout its range, and has been designated a "Bird of Conservation Concern" (U.S. Fish and Wildlife Service 2002). The range of the species has contracted greatly over the past half-century (Cade and Woods 1997), and Christmas Bird Count and Breeding Bird Survey data indicate a continent-wide decrease in abundance. The sharpest declines have occurred in the core of the shrike's range in southern and Gulf Coast areas (Yosef 1996).

Most studies of Loggerhead Shrikes have revealed high nest success (mean of 56%; Yosef 1996, Esely and Bollinger 2001), suggesting that problems associated with winter habitat and survival may be causes for population declines (Haas and Sloane 1989, Brooks and Temple 1990, Gawlik and Bildstein 1993). Based on reports of high nest success throughout the species' range, Maddox and Robinson (2004) considered it fortuitous that habitat degradation had not resulted in elevated rates of nest predation or decreased productivity. Our observations, and the results of some, more recent studies (DeGeus 1990, Yosef 1994, Collins 1996, Esely and Bollinger 2001), suggest there are landscapes and nest-site contexts in which this presumption does not apply. Our objectives were to measure nest success of Loggerhead Shrikes in a region of intensive agriculture with marginal habitat, and to determine whether land use near nests, or nest-site context, influenced nest fate.

METHODS

From 1998 through 2000, we monitored Loggerhead Shrike nests within a 125-km^2 area of southern Jasper County, Illinois. The study was centered on Prairie Ridge State Natural Area (88° 12′ W, 38° 57′ N) and included most of Smallwood Township and adjacent portions of Wade and Fox townships. Jasper County's landscape is composed of 71% row crop (corn, *Zea mays*; and soybeans, *Glycine max*), 6% wheat (*Triticum aestivum*; most double-cropped to soybeans after harvest), 6% rural grassland (hay, pasture, roadsides, and idle grass), 13% woodland, and 1% roads, residential/urban areas, and small amounts of open water and other land covers (Illinois Interagency Landscape Classification Project 2002). Our study area differed from the county as a whole by having greater row crop cover (>85%) and less woodland cover (<5%; JWW unpubl. data).

Between 1966 and 2000, North American Breeding Bird Survey results suggested declining abundance of Loggerhead Shrikes in Illinois (−4.5%/year) and the Midwest (−0.3%/year in the eight states of U.S. Fish and Wildlife Service Region 3; Sauer et al. 2005). From 1994 to 1996, roadside searches

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within 49 km^2 of the center of our 1998–2000 study area documented 12 (1996) to 16 (1994) shrike territories annually (roughly 0.25–0.33 shrike territories/km^2; JWW unpubl. data, reported to the Illinois Department of Natural Resource's Natural Heritage database). During our 1998–2000 study, the densities of nesting shrikes were similar to, or lower than, that reported during the 1994 to 1996 roadside surveys.

From March through June, we located shrike nests by locating adults or food caches, searching nearby suitable nest sites, observing nest building, or observing provisioning of incubating females and nestlings. Because the study area was almost entirely private land, initial searches were limited to roadsides. When shrikes were located, we often were permitted to search for, and monitor, nests on private land. We checked nests every 3–5 days until their fate was determined, and we calculated nest and egg success based on exposure days (Mayfield 1975, Johnson 1979). When nests failed, we assumed failure occurred at the midpoint between nest checks.

We recorded nest context and visually estimated the percentage of land-use types within 100 m (3.1 ha) of nest sites (after Gawlik and Bildstein 1993). Land-use categories were (1) row crop; (2) hay or pasture; (3) idle grassland; (4) woody vegetation (forest and shrub areas combined); (5) small grains; (6) roadways, including grassy rights-of-way; and (7) residential (yards and farmsteads). We compared measurements at nest sites with 20 random locations, each also 100 m in radius and selected by overlaying a map of the study area with a numbered grid. Because shrike nest sites are limited to woody vegetation, we centered random locations on the tree or shrub closest to each randomly selected point. We characterized the context of nest sites and random trees as follows: fencerows, farmsteads/yards, watercourses, woodland edges, or isolated trees (>20 m from another tree). Because the proportions of land uses were not normally distributed across the study area, we used Mann-Whitney *U*-tests to compare land use between random sites and nest sites, and between successful and depredated nests. Contexts of nest trees and random trees, and trees with successful and depredated nests, were compared using a chi-square test. Unless otherwise noted, values are reported as means ± SE.

RESULTS

We monitored 34 shrike nests from 1998 through 2000. Ten nests (29%) fledged ≥1 young, 21 nests (62%) were depredated, 2 (6%) were abandoned during egg laying, and 1 (3%) was dislodged from a tree during a thunderstorm. Nest failures attributed to predation included 6 empty nests with no evidence of the predator, 4 tilted or compressed nests, and 11 highly disturbed nests (lining removed, nest shredded, or completely dislodged). At one depredated nest on a farmstead, the cooperators reported to us that their domestic cat (*Felis cattus*) had killed one of the adults. Shrike nests appeared to be more vulnerable to predation near hatching. Of 22 nests surviving to at least the 14th day of incubation, 8 were eventually lost to predators before the nestlings were 4 days old.

From the beginning of egg laying to fledging, egg success was 20.5% and nest success was 25.6% (95% CI = 19.4–33.8%). Clutch size was 5.7 ± 0.2 eggs (n = 30 nests). In nests that survived until at least the second nest check after hatching, 87.5 ± 3.6% of eggs hatched successfully (n = 10 nests). Although 4.4 ± 0.4 young fledged per successful nest, only 1.3 ± 0.4 young fledged per nest attempt.

Land use within 100 m of shrike nests included more hay and pasture than randomly located points (Mann-Whitney $U = 241.0$; $P = 0.049$), but no other variable that we measured differed between nest and random locations (Table 1). Land use did not differ significantly between successful and depredated nest sites. The majority of the nests we monitored (87%) were located in small (<3 ha) pastures (including the enclosing fences) or yards/farmsteads, and were within 50 m of county roads. Although shrike nests were placed in fencerows more frequently than expected ($\chi^2 = 25.69$, df = 4, $P < 0.001$), nests in fencerows were more likely to be depredated ($\chi^2 = 10.94$, df = 3, $P = 0.012$; Table 2). Daily nest survival was 0.957 ± 0.012 in fencerows and 0.973 ± 0.013 in yards/farmsteads.

TABLE 1. Percent land use (± SE) within 100 m (3.1 ha) of random trees and Loggerhead Shrike nest locations in Jasper County, Illinois, 1998–2000.

Land use	Random sites (n = 20)	Nest sites All (n = 33)	 Successful (n = 10)	 Depredated (n = 21)
Row crops	58.6 ± 6.9	51.0 ± 4.9	51.3 ± 9.2	54.4 ± 6.1
Hay and pasture	7.5 ± 4.7	19.4 ± 4.9[a]	18.5 ± 9.5	19.3 ± 5.9
Idle grassland	10.5 ± 6.0	5.9 ± 2.6	6.0 ± 5.1	6.4 ± 3.5
Woodland	7.2 ± 2.9	2.6 ± 0.9	3.0 ± 1.9	1.8 ± 0.5
Small grains	2.8 ± 1.6	3.2 ± 1.6	0.0 ± 0.0	2.9 ± 2.0
Roadway	5.8 ± 1.4	9.5 ± 1.3	7.5 ± 2.0	10.2 ± 1.8
Farmstead, yard	7.3 ± 2.2	8.8 ± 2.4	13.0 ± 5.4	7.6 ± 2.8

[a] Significantly more hay and pasture at nest sites than random sites (Mann-Whitney U = 241.0, P = 0.049). There were no other significant (all $P >$ 0.08) differences in land use between random and nest sites or between successful and depredated nests.

DISCUSSION

Reproductive success of Loggerhead Shrikes in this agricultural landscape (25.6% nest success, 20.5% egg success) is among the lowest reported for the species. Graber et al. (1973) reported 80% nest success in southeastern Illinois in 1967 and, in Jasper and nearby counties, Anderson and Duzan (1978) observed 72% nest success in 1971–1972. By 1991–1992, Collins (1996) found that the proportion of fledglings to number of eggs laid had dropped to 25% in southern Illinois. Our methods for measuring nest success (Mayfield 1975) differ from that used by Collins (1996), but the results are similar and suggest a substantial reduction in shrike nesting success in the region.

Clutch size (5.7 eggs) in our study was similar to those of recent Midwestern studies (5.3–5.7 eggs; Burton 1990, DeGeus 1990, Collins 1996, Esely and Bollinger 2001). Our measure of 4.4 fledglings per successful nest was the same as the mean reported from 14 studies compiled by Esely and Bollinger (2001). Toxicological problems affecting egg viability are not implicated; an analysis of organochlorine residues in shrike eggs, including several eggs collected in our study area in 1995 and 1996, indicated that DDE levels had decreased 79% in the region since the early 1970s (Anderson and Duzan 1978, Herkert 2004). Roughly 88% of fully incubated eggs hatched successfully during our study.

TABLE 2. Proportions of Loggerhead Shrike nests and random tree locations within various land-use contexts in southeastern Illinois, 1998–2000.

Context	Random sites (n = 20)	Nest sites All (n = 34)	 Successful (n = 10)	 Depredated (n = 21)
Yard, farmstead	0.35	0.24	0.40	0.14
Fencerow	0.20	0.53[a]	0.30	0.62[a]
Watercourse	0.15	0.15	0.20	0.14
Woodland edge	0.15	0.00	0.00	0.00
Isolated tree	0.15	0.09	0.10	0.10

[a] Loggerhead Shrike nests were placed in fencerows more frequently than expected (χ^2 = 25.69, df = 4, $P <$ 0.001), and nests in fencerows were more likely to be depredated (χ^2 = 10.94, df = 3, P = 0.012).

Intensified agricultural land use and a concomitant increase in the abundance of generalist predators are likely the causes for a decrease in shrike nesting success in this landscape. Predation was implicated in 88% of the nest failures and in 62% of all nesting attempts in our study. From 1970 to 2000, acreage of row crops increased by 26% in Jasper County, while hay acreage decreased by 85% and pasture decreased by about 47% (Illinois Department of Agriculture 1971, National Agricultural Statistics Service undated). Potential nest sites in this landscape are few and most occur in linear habitats, often limiting shrikes and other birds to nesting situations in prey-rich corridors that are easily searched by predators (Major et al. 1999). Furthermore, human structures and agricultural waste may subsidize populations of generalist predators (Warner 1985, Dijak and Thompson 2000). Road-kill surveys conducted by the Illinois Department of Natural Resources from 1975 through 1998 documented increases in the abundance of raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) of more than 250% and 100%, respectively (Gehrt et al. 2002; S. D. Gehrt pers. comm.).

Successful shrike nests were more likely to be in yards, whereas depredated nests were more likely to be in fencerows. Yards are not benign breeding habitat, however. Gawlik and Bildstein (1990) recognized the potential threat of predation by domestic cats on adult shrikes and their young, and during our study, a cat killed at least one yard-nesting adult shrike. Row crops were the most common land use near nests, reflecting the ubiquitousness of cropland in the landscape, but shrikes preferentially selected nest sites in or near pastures (Table 1). Most pastures in our study area were small (<3 ha) horse pastures adjacent to residences, which were located primarily along county roads. Shrikes elsewhere also frequently nest near roadsides, and the shorter grasses and utility lines along roadsides may be superior hunting areas (Luukkonen 1987, DeGeus 1990, Gawlik and Bildstein 1990, Smith and Kruse 1992). The visibility of shrikes on utility lines (i.e., along roads) may have contributed to high representation of pasture habitat near the shrike nests that we monitored, but little suitable nesting habitat was available to Loggerhead Shrikes away from roadways in our study area. Although widely used, roadways and other linear habitats may be ecological sinks for nesting shrikes, given the low nesting success we found and that has been reported elsewhere. Yosef (1994) found lower nest success among shrikes nesting in fencerows (36%) than for those nesting within pastures (54%) in Florida. Likewise, roadside-nesting Loggerhead Shrikes had 39% nest success in Missouri (compared with 76% success for interior nests; Esely and Bollinger 2001), 35% nest success in Iowa (DeGeus 1990), and 31% egg success in Indiana (Burton 1990).

Pasture and hay acreage has declined by 50% in the Midwest over the past 50 years (Herkert et al. 1996). At the same time, shrikes have declined or disappeared from much of the region (Cade and Woods 1997, Sauer et al. 2005). Our results—documenting a sharp decrease in nesting success in a county with recent land-use changes typical of the Midwest—suggest that nesting success, often thought to be relatively high for shrikes (Yosef 1996, Maddox and Robinson 2004), will need to be re-evaluated as land-use changes result in a less optimal environment for Loggerhead Shrikes.

ACKNOWLEDGMENTS

We thank the many private landowners of Jasper County, Illinois, who permitted us to access their properties to search for and monitor nests. This project was supported by an S. Charles Kendeigh Award from the Champaign County Audubon Society, and the University of Illinois. R. Yosef, C. P. Woods, and anonymous reviewers suggested several improvements to the manuscript.

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The Wilson Journal of Ornithology 118(1):75–80, 2006

NEST INTERFERENCE BY FLEDGLING LOGGERHEAD SHRIKES

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ABSTRACT.—Using video cameras, we documented at least two fledgling Loggerhead Shrikes (*Lanius ludovicianus*) visiting their parent's second active nest. We recorded 70 visits during a 10-day period, with visits averaging 7 min. We observed the fledglings sitting on the nest contents on 21 occasions. We concluded that these visits were not indicative of cooperative breeding behavior, because the fledglings were destructive to the nest structure and contents, and the adult female exhibited aggressive behavior toward the fledglings. An early reduction in post-fledging parental care by their father (who was of captive-bred origin) and slow development of the fledglings' hunting skills might have caused them to seek food resources from their mother. However, this is the first time that we have observed these behaviors in this intensively managed population. *Received 27 December 2004, accepted 24 October 2005.*

The presence of extra individuals at nests has been observed in many groups of birds (Skutch 1961, Stacey and Koenig 1990). Many of these extra individuals have been considered "helpers" in cooperative breeding systems. Helpers have been documented in a variety of species, including members of the Corvidae (Woolfenden and Fitzpatrick 1984), Hirundinidae (Myers and Waller 1977, Fraga 1979), Furnariidae (Skutch 1969), and a few raptors (Faaborg et al. 1980, James and Oliphant 1986). These extra individuals are considered to place the good of the species over the good of the individual, contrary to the basic tenets of natural selection (Wynne-Edwards 1962). In these systems, the extra individuals help a breeding pair maximize annual productivity by assisting with nest building, attendance, and post-fledgling care.

However, not all extra nest visitors can be classified as helpers. Lombardo (1986) noted that the sole purpose of extra Tree Swallows (*Tachycineta bicolor*) visiting a breeding pair's nest was to obtain food resources. House Wrens (*Troglodytes aedon*) and Acorn Woodpeckers (*Melanerpes formicivorus*) have been observed using their non-active natal nests for night roosting (Preble 1961, Koenig et al. 1995), and fledgling Carolina Wrens (*Thryothorus ludovicianus*) have used an active Northern Cardinal (*Cardinalis cardinalis*) nest during a period of inclement weather (Jawor and Gray 2003). Thus, the motivation for visiting the active nests of parents or unrelated adults likely varies by species.

As part of a larger study assessing the nesting behavior of Loggerhead Shrikes (*Lanius ludovicianus*) on San Clemente Island (SCI), California, we documented at least two fledglings from a first brood visiting and interfering at their parent's second nest. We believe this is the first record of fledgling shrikes returning to their parent's subsequent active nest. We document the nest visitation by these fledglings, and explore the reasons for these visits.

METHODS

We collected our fledgling interference data during a larger study on the nesting behavior of Loggerhead Shrikes on SCI (32° 50′ N, 118° 30′ W), which is located approximately 109 km northwest of San Diego, California. SCI is administered by the U.S. Navy and is used for active military training as part of the Southern California Offshore Range; the U.S. Navy also has an environmental program on the island for the protection and conservation of natural resources (U.S. Department of the Navy 2002).

From 23 May to 27 June 2003, we videotaped a pair of shrikes nesting in Norton Canyon, located on the west side of SCI. The breeding territory at this site is at the bottom of a steep canyon, where there are several small trees and shrubs. As part of the recovery program for this endangered population, two captive-born shrikes were released into the wild in 1999 (male) and 2001 (female) as hatch-year birds. In 2002, the male bred successfully in this same territory, whereas the female bred successfully with another male in

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a nearby canyon in 2002. As part of the larger recovery effort to improve reproductive output and survival of adults and offspring, we provided supplemental food to these birds every other day during the breeding season (i.e., 1 February–15 July; feeding began when birds took up occupancy at this site). We provided a diet of mealworms (*Tenebrio* sp.), crickets (*Gryllus* sp.), mice (*Mus musculus*), and lizards (*Anolis* sp.) in plastic tubs that we lowered by rope into the canyon bottom, where they remained for the adults to use for a 1-hr period. During this 1-hr period, we recorded data on the identity, health, and behavior of all shrikes present; the amount of supplemental food taken; and what each individual did with the supplemental food (e.g., cached the food, fed themselves, male fed the fledglings or the female on the nest).

To assess the behavior of nesting shrikes, we used miniature video cameras (model MVC2000-WP-LED, Micro Video Products, Bobcaygeon, Ontario, Canada; 7.5 × 4 cm) placed within 30 cm of the nest. We set up cameras during the egg-laying stage. Each camera was equipped with infrared light-emitting diodes to allow data collection during night hours. We used coaxial cable to connect each camera to a time lapse VCR located ~500 m from the nest tree. We powered the VCR and camera with a series of 12-volt deep-cycle marine batteries and used solar panels to maintain battery charge. We programmed each VCR to record five frames/sec, and we changed the video tape every 24 hr. We reviewed video tapes later to record nesting activity. We also recorded any unusual events at the nest, such as the presence of predators or competitors and the interactions (aggressive or not) between the male and female. We considered behaviors such as bill snapping and physical contact as aggressive behaviors (Yosef 1996). We collected other nesting behavior data from this site by observing the territory from the canyon rim during supplemental feeding sessions (i.e., every other day). All results are presented as means ± SE.

RESULTS

Five young fledged from the first nest on ~6 May. All fledglings were color banded prior to fledging for individual identification. Both adults provided care to the fledglings until ~23 May, when the female began incubating her second clutch in a different tree within the same territory. Data collected during supplemental feeding observations indicated that three to four fledglings were present at the second nest site during the period we collected video data. We also found that the male allocated more time to feeding the female on the second nest than to caring for the first-nest fledglings.

During the second nest attempt (23 May–27 June), from which five young fledged, we observed at least two different first-nest fledglings visiting the second nest on 10 different days. Color bands were indistinguishable on black-and-white video footage, but we had verified the identity of first-nest fledglings remaining in the territory during supplemental feeding sessions. The first visit was made on 24 May and the last took place on 8 June, although we detected at least three fledglings from the first nest attempt in the general area until 11 July. We do not know whether fledglings were regularly present in the nest tree during this period, as the camera was focused on the nest and immediate surroundings. On numerous occasions, the adult female was observed vocalizing at something in the nest tree, probably fledglings that may have spent considerable time in the nest tree and out of camera view.

We recorded 70 visits (mean visits/day = 7.0 ± 2.4, range = 1–22) during the 10 days when first-nest fledglings appeared at the nest (Fig. 1). During these visits, fledglings spent a total of 6 hr 48 min at the nest (mean min/visit = 7.0 ± 1.7, range = 3–21). On 24 May, two first-nest fledglings were present at the nest at the same time on three separate occasions. Subsequently, we witnessed only one fledgling at the nest at any one time.

On 21 occasions, we observed a first-nest fledgling sitting on the nest while the adult female was away. This occurred 16 times during the egg stage and 5 times during the nestling stage. When the female left the nest, the fledgling would move into the nest cup immediately. The total time spent sitting on the nest contents by first-nest fledglings was 1 hr 12 min, averaging 3.0 ± 1.0 min per occasion. On two occasions when a fledgling was sitting on the nest, the female tried to evict the fledg-

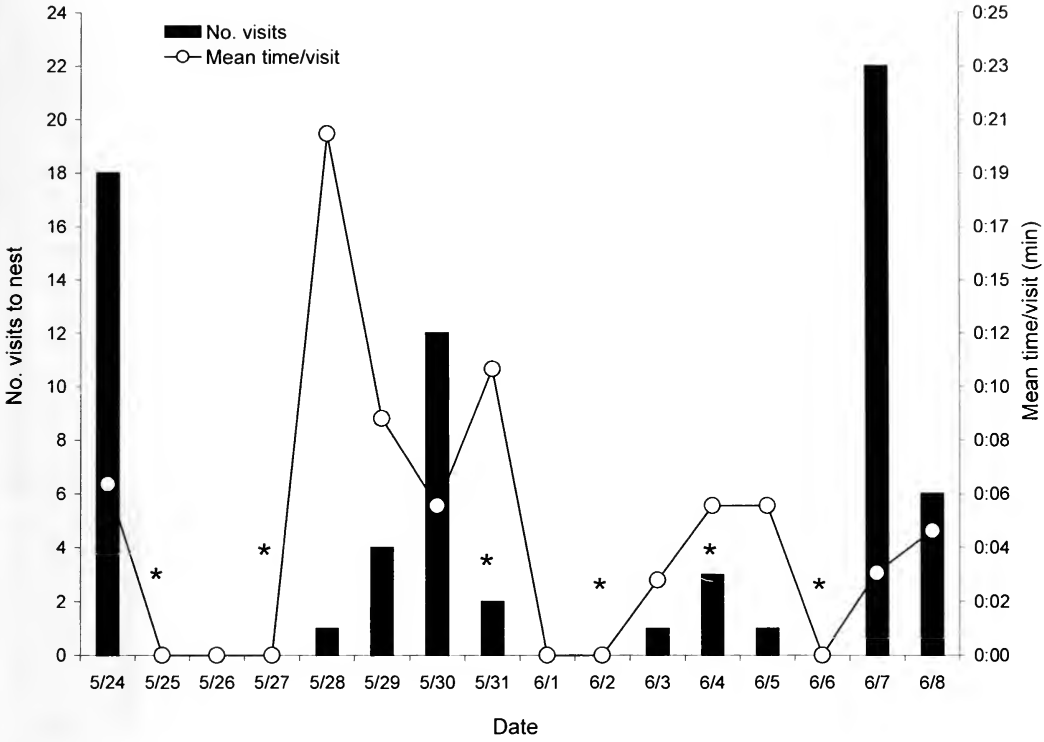

FIG. 1. Number of visits and mean time per visit for fledgling Loggerhead Shrikes returning to their parents' second active nest on San Clemente Island, California, 2004. Asterisks indicate dates when we provided supplemental food.

ling by pecking at it. During one visit, the female sat on top of the fledgling for 15 min, poking underneath the fledgling as if to check on her eggs. On several occasions, the fledgling would act destructively while sitting on the nest. These behaviors included pulling up the nest lining, pulling sticks out of the nest structure, breaking open an egg and eating the eggshell, pecking at newly hatched nestlings, and stealing food from the female. Other behaviors exhibited by fledglings included constant begging to the female, sleeping on the rim of the nest, and blocking the female from entering the nest cup. Fledglings would block the female by getting in the nest and moving so that the female could not resume incubation or brooding.

We observed the adult female feeding first-nest fledglings on 18 occasions (Fig. 2), not including when fledglings stole food from the female or consumed food laying in the nest. More often, however, the female was aggressive toward fledglings at the nest. We recorded 215 aggressive acts between the female and fledglings, with the number of aggressive acts/min ranging from 0.25 to 1.16 (Fig. 2).

DISCUSSION

We believe this is the first report of fledgling shrikes returning to an active nest of their parents. The actual number of different fledglings visiting the nest (we know of at least two) was uncertain. It does seem clear, however, that the observations made at this nest are not behaviors associated with a cooperative breeding system. In cooperative breeding systems, helpers are present to assist the nesting pair increase productivity (Skutch 1961). Assisting with nest building, nest defense, nest attendance, and post-fledging care allows the nesting pair to focus their energy on producing multiple clutches. Some species would not be capable of double-clutching without a cooperative breeding system (Poiani and Jermiin 1994). Although Loggerhead Shrikes on SCI are frequently double-brooded, in this

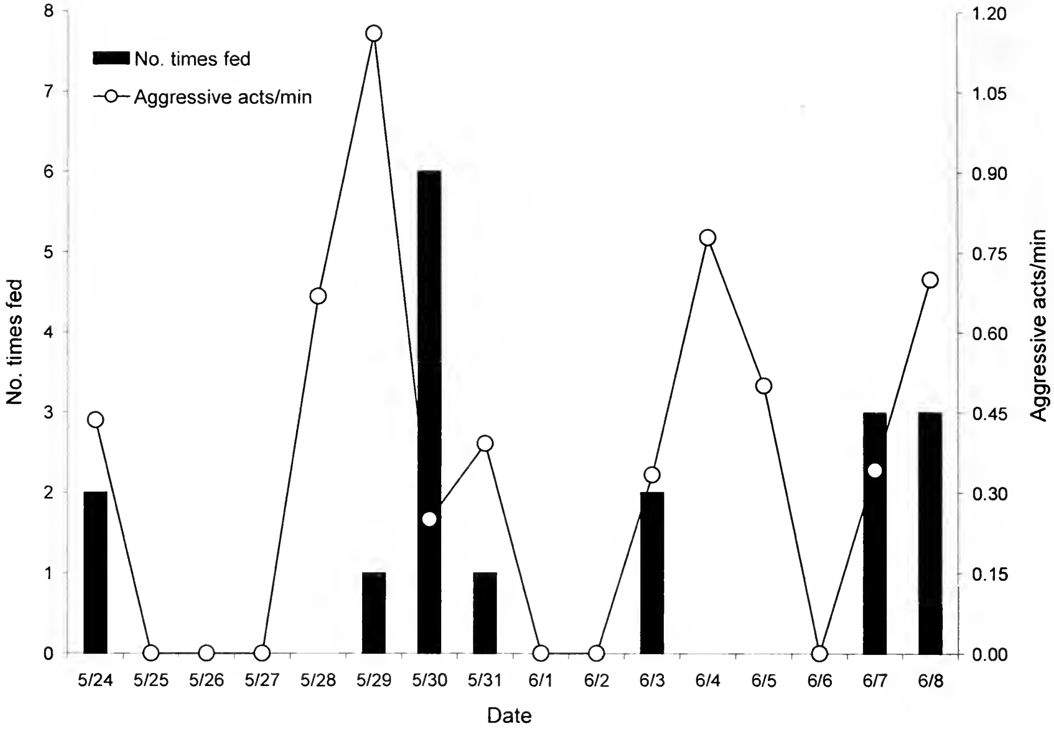

FIG. 2. Number of times fledglings were fed by their parents while visiting their second nest, and the number of aggressive acts per minute exhibited by the adult female toward visiting fledglings while at the nest, San Clemente Island, California, 2004.

case, the destructive nature of these fledglings (e.g., nest and egg destruction, attacking nestlings, stealing food) suggests that they were not attempting to increase their parent's annual productivity, despite their incidental nest attendance.

We believe first-nest fledglings visited the nest and begged from the female to extend parental care. In Loggerhead Shrikes, post-fledging care is generally the duty of the male (Yosef 1996). During this period, the male provisions the young, who often follow the male around, presumably learning how to hunt for food. This period extends to independence, which occurs 40 days after hatching (Scott and Morrison 1990). The first-nest fledglings in our study should have become independent on 29 May. However, it appears that when the female began incubating her second clutch on 23 May, the male turned his attention to provisioning the female on the nest and reduced his feeding of the first-nest fledglings. Therefore, it appears that the amount of parental care might have been reduced earlier than normal, although how and when parental care is terminated remains unclear. Trivers (1974) suggests that there is a conflict between adults and offspring regarding how long the dependency period should be. There should be selective pressure for young to try to receive more parental care than is optimal for the parents to give.

Why males might reduce parental care early is unknown. The male we observed was captive-bred and may have exhibited some behavioral abnormalities associated with being reared in captivity. Selection pressures in captivity are vastly different from those in the wild, and, as a result, changes in important life-history behavioral traits may occur (Curio 1996, McPhee 2003). For example, Woolaver et al. (2000) found that over-dependence on food provisioning resulted in behavioral changes in captive-bred and released Echo Parakeets (*Psittacula echo*), and Harvey et al. (2002) found abnormal nesting behavior in captive Hawaiian Crows (*Corvus hawaiiensis*). Thus, since the male we observed was reared in captivity before being released into the wild, there could have been some behavioral deficiency causing the male to terminate parental care prematurely. We do not believe this to be the case, however, as this male was released into the wild as a juvenile, and young birds are better at assimilating into new wild environments than adults (Swinnerton et al. 2000, Robert et al. 2004, Turner et al. 2004). In addition, this male bred each year after his release and successfully raised four fledglings to independence prior to 2003. During nest monitoring of his prior breeding attempts, we did not detect any abnormal behavior (Institute for Wildlife Studies unpubl. data).

A more plausible explanation for our unusual observation could be the presence of supplemental food provided as part of the recovery program. Supplemental food is meant to increase survival and productivity; however, it is unknown to what extent released birds rely on this food. If the male shrike relied on supplemental food for provisioning the female and fledglings, he may have foraged less for natural food than birds that do not receive supplemental food. It is also possible that the presence of supplemental food slowed the first-nest fledglings' learning process in acquiring natural food. Wheelwright and Templeton (2003) suggest that the speed at which juveniles acquire foraging skills might determine the length of parental care. By feeding regularly from the food tubs, the fledglings may not have observed many wild foraging tactics by the male. Thus, they needed more time to develop these skills and continued to beg for food from both adults—despite the potential cost to the adults (Trivers 1974).

Our supplemental feeding observations revealed that first-nest fledglings learned to forage from the food tubs rather quickly and regularly took supplemental food when we offered it. This may explain why the fledglings did not visit the second nest every day. We provided supplemental food on 6 days during the period when the fledglings were observed at the nest (24 May–8 June). They did not visit the nest on 4 of those days (25 May, 27 May, 2 June, 6 June), and visited only two or three times on each of the other 2 days we provided supplemental food (31 May and 4 June; Fig. 1). Fledglings visited the nest on 8 of 10 days when food was not provided, suggesting that the fledglings sought provisioning from the female.

Differences in the number of visits each day could also be explained by the abrupt reduction in food provisioning. The first day the female ceased parental care for her first brood was 24 May. The fledglings were unaccustomed to not being fed by her, potentially explaining the 18 visits to the nest on that day (Fig. 1). On 7 June, the second clutch of eggs began to hatch, and there was a spike in activity surrounding the nest as the female removed eggshells and began feeding newly hatched chicks. This increase in activity, especially with food deliveries to the nest, may have caused the high number of visits recorded (n = 22; Fig. 1) that day.

In general, we believe that the visits of these fledgling shrikes to their parent's second nest were motivated by hunger, possibly due to early reduction of parental care or the retardation of foraging skills due to the presence of supplemental food. On SCI, all captive-reared pairs released into the wild received supplemental food. Since 2003, we have placed small video cameras at 10 shrike nests to study nesting behavior, and have not observed nest visits by first-nest fledglings at any other time (Institute for Wildlife Studies unpubl. data).

Despite the potential benefit provided by fledglings "tending" the nest when the adult female was away from the nest, the first-nest fledglings likely interfered with the success of the second nesting attempt, as one egg was destroyed by a visiting fledgling, food was stolen from the female, and visiting fledglings constantly pecked at newly hatched young.

ACKNOWLEDGMENTS

We thank D. M. Cooper, R. Dempsey, and C. Campbell for assisting with the implementation of the camera systems and initial review of video tapes. We thank the Shrike Working Group, consisting of the U.S. Navy, U.S. Fish and Wildlife Service, PRBO Conservation Sciences, and the Zoological Society of San Diego, for their input regarding the initial use of the video cameras at shrike nests. We thank the biologists from PRBO Conservation Sciences for their assistance in monitoring shrike nests before and after the installation of nest cameras. We also thank the shrike release crew of the Institute for Wildlife Studies for monitoring shrikes at our camera site during supplemental feeding sessions. E. M. Russell and two anonymous referees provided comments on an earlier draft of the manuscript.

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The Wilson Journal of Ornithology 118(1):81–84, 2006

FIRST BREEDING RECORD OF A MOUNTAIN PLOVER IN NUEVO LEON, MEXICO

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ABSTRACT.—We document the first breeding record of Mountain Plovers (*Charadrius montanus*) in the state of Nuevo Leon, Mexico. On 9 July 2004, we located a nest with two eggs and one chick in a colony of Mexican prairie dogs (*Cynomys mexicanus*). Mean height of vegetation near the nest was 7.1 cm, and bare ground cover was 41.2% (30 m^2 sampled). Although this record represents the second nesting for this species in Mexico, it is the first to document successful breeding. *Received 21 January 2005, accepted 5 November 2005.*

The Mountain Plover (*Charadrius montanus*) is a species of North America's grasslands. It is classified as vulnerable on the IUCN Red List (Birdlife International 2004), endangered in Canada (Committee on the Status of Endangered Wildlife in Canada 2004), and threatened in Mexico (Diario Oficial de la Federación 2002). In the United States, the Mountain Plover was proposed for listing as a threatened species in 1999 (U.S. Fish and Wildlife Service 1999), but the proposal was withdrawn in 2003 (U.S. Fish and Wildlife Service 2003). The U.S. Shorebird Conservation Plan rates the species as highly imperiled (Brown et al. 2001). Between 1966 and 1991, the entire population of Mountain Plovers declined by 63% (Knopf 1994); currently, the population is estimated at 11,000–14,000 individuals (Plumb et al. 2005). The population decline has been attributed to loss of nesting habitat due to cultivation, urbanization, livestock management, and declines in native herbivores, mainly black-tailed prairie dogs (*Cynomys ludovicianus*) and North American bison (*Bison bison*; Wiersma 1996, BirdLife International 2004).

The Mountain Plover's primary breeding range includes eastern Colorado, central Wyoming, eastern Montana (Graul and Webster 1976), northeastern New Mexico, and the Oklahoma and Texas panhandles (Knopf 1996). An isolated breeding population, which may be resident year-round, occurs in the Davis Mountains, Texas (Knopf 1996). In the United States, the plover's winter range extends from Sacramento, San Joaquin, and the Imperial Valley in California east to the Lower Colorado River Valley, and from Yuma east to Phoenix and the Chandler area in southern Arizona (Rosenberg et al. 1991, Knopf and Rupert 1995). In Mexico, the winter distribution has not been well studied, but it is believed to extend along the U.S./Mexico border south through Baja California, Sonora, Chihuahua, and Tamaulipas into Zacatecas and San Luis Potosí (Phillips et al. 1964, Wilbur 1987, Howell and Webb 1995, Gomez de Silva et al. 1996). More surveys are needed to document wintering as well as year-round resident populations.

Mountain Plovers nest in shortgrass and mixed grass prairies (Graul and Webster 1976, Knowles et al. 1982, Knopf and Miller 1994, Knopf and Rupert 1999b). They typically occur in areas characterized by short vegetation (<8 cm high; Graul 1975) and ≥30% bare ground (Knopf and Miller 1994), and they are commonly associated with prairie dog colonies (*Cynomys* spp.; Knowles et al. 1982). Vegetation at nest sites varies throughout the breeding range, but is usually dominated by blue grama (*Bouteloua gracilis*), buffalograss (*Buchlöe dactyloides*), needle-and-thread (*Stipa comata*), and sagebrush (*Artemisia* sp.; Finzel 1964, Graul 1975, Knowles et al. 1982, Knopf and Miller 1994). Plovers often nest near cow manure, rocks, or clumps of vegetation (Graul 1975, Olson and Edge 1985, Knopf and Miller 1994).

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During the breeding period, Mountain Plovers have been observed in colonies of Mexican prairie dogs (*Cynomys mexicanus*) around San Juan del Prado, Galeana, Nuevo Leon. These observations have included individuals in breeding plumage and birds exhibiting reproductive behavior (calls, displays, etc.; Knopf and Rupert 1999a). On 5 July 1994, observers found six widely spaced pairs and one single individual; on 16 June 1997, seven individuals (including a pair) were detected in three unspecified prairie dog colonies in the same area; and on 24 April 1998, seven more individuals (including two pairs) were observed. Mountain Plovers were also detected on 25 April 1998 at Galeana between El Cristal and La Paz (two pairs and two territorial males) and on 26 April 1998 at La Hediondilla (one pair and one single) and Llano La Soledad (two pairs), where unsuccessful attempts were made to document nesting (Knopf and Rupert 1999a). During 5–11 May 1999, Desmond and Chavez-Ramirez (2002) observed 30 Mountain Plovers, including eight pairs and two groups of three individuals each at Rancho Los Angeles and La India, in Saltillo, Coahuila de Zaragoza, and at La Casita in Galeana, Nuevo Leon. On 9 May 1999, Desmond and Chavez-Ramirez (2002) found a nest with three eggs near La India, the only previous nest documented in Mexico. The La India nest was not monitored and therefore, its outcome is unknown. Previous nest searches conducted in Mexico during the plover's known reproductive period (based on observations in the Great Plains) yielded no other nesting records; however, Desmond and Chavez-Ramirez (2002) suggested that the breeding season in northeastern Mexico might be later than it is farther north so that hatching coincides with the rainy season and the period of greatest insect availability (June–July).

On 9 July 2004, around 17:00 CST, we observed a Mountain Plover pair at Llano La Soledad, a gypsophile grassland (7,607 ha) within ejido San Rafael, Galeana, Nuevo Leon (24° 48′ 50″ N, 100° 41′ 54″ W). Llano La Soledad contains the largest known colony of Mexican prairie dogs (Treviño-Villarreal and Grant 1998). As we approached the pair, one individual feigned wing injury, while the other emitted alarm calls and flew around us. After a few minutes, one individual "squatted" on the ground, placed its bill under its body, and remained motionless. When we approached within 2 m of what appeared to be a nest, the bird again feigned wing injury. We subsequently located the nest, which contained two eggs and one chick. The chick remained motionless while the adults called (as described by Graul 1974).

Relative to the plover's nest, the nearest Mexican prairie dog burrow was approximately 15 m away. There was also a small cluster of *Atriplex* shrubs (*n* = 28; estimated mean height = 60 cm) 40 m from the nest. Livestock (cattle, goats) were nearby, but the area was not overgrazed, nor was cow manure found near the nest. We photographed and video-recorded the nest. This record represents the first Mountain Plover nest in Nuevo Leon, and the first record of successful nesting for Mountain Plovers in Mexico.

As part of another study at Llano La Soledad, we had characterized the vegetation a few days prior to finding the plover nest. After finding the nest, we selected three of our 1 × 10-m quadrats that were closest to the nest—200, 1,000, and 1,500 m away—to characterize the vegetation. We recorded height, cover diameter, and species of each plant. We then calculated mean height, relative density (RD = number of individuals of a given species as a proportion of the total number of individuals of all species), relative frequency (RF = frequency of a given species as a proportion of the sum of the frequencies for all species), relative coverage (RC = coverage for each species expressed as a proportion of the total coverage for all species), and importance value of each species (IV = RD + RF + RC, which provides an overall estimate of the influence or importance of a plant species in the community; Brower et al. 1990; Table 1). We identified 11 plant species, with a mean height of 7.1 cm. The most common forbs were summer bluet (*Hedyotis purpurea*; *n* = 725, RD = 37, RF = 15.9) and McVaugh's bladderpod (*Leonsquerella mcvaughiana*; *n* = 273, RD = 13.9, RF = 15.9); *Muhlenbergia* sp. (*n* = 654, RD = 33.3, RF = 15.9) and Karwinski's grama (*Bouteloua karwinskii*; *n* = 140, RD = 7.1, RF = 10.5) were the most common grasses. *Muhlenbergia* sp. had the greatest RC (43.3%) and IV (92.3), and the IV of summer

TABLE 1. Vegetation composition and structure in three 1 × 10-m quadrats, placed 200, 1,000, and 1,500 m away from a Mountain Plover nest, in the grassland at Llano La Soledad, Galeana, Nuevo Leon, Mexico, July 2004.

Species	No.	H[a] (cm)	RD[b] (%)	RF[c] (%)	RC[d] (%)	IV[e]
Forbs						
Summer bluet (*Hedyotis purpurea*)	725	2.5	37.0	15.9	12.4	65.2
McVaugh's bladderpod (*Lesquerella mcvaughiana*)	273	3.3	13.9	15.9	19.0	48.8
Desert zinnia (*Zinnia acerosa*)	80	4.5	4.0	5.3	5.7	15.0
Woody crinklemat (*Tiquilia canescens*)	47	5.8	2.4	5.2	3.7	11.3
Houston machaeranthera (*Machaeranthera aurea*)	35	5.1	1.7	5.2	0.5	7.4
Texas sundrops (*Calylophus tubicula*)	5	8.6	0.3	10.5	0.7	11.5
Slimpod fiddleleaf (*Nama stenophyllum*)	1	3.0	0.1	5.2	0.1	5.4
Grasses						
Muhly (*Muhlenbergia* sp.)	654	5.3	33.3	15.9	43.3	92.3
Karwinski's grama (*Bouteloua karwinskii*)	140	1.7	7.1	10.5	13.0	30.6
Havard's threeawn (*Aristida havardii*)	1	25.0	0.1	5.2	1.2	6.5
Buffalograss (*Buchloë dactyloides*)	1	13.0	0.1	5.2	0.4	5.7

[a] H = mean height.
[b] RD = relative density (number of individuals of a given species as a proportion of the total number of individuals of all species).
[c] RF = relative frequency (frequency of a given species as a proportion of the sum of the frequencies for all species).
[d] RC = relative coverage (coverage for each species expressed as a proportion of the total coverage for all species).
[e] Importance value = RD + RF + RC (Brower et al. 1990).

bluet was 65.2. The sampled area comprised 41.2% bare ground.

The continued documentation of Mountain Plover nests in northeastern Mexico further confirms that a breeding population of Mountain Plovers exists in northeastern Mexico (Knopf and Rupert 1999a, Desmond and Chavez-Ramirez 2002). Desmond and Chavez-Ramirez (2002) proposed that the breeding season in northeastern Mexico may be later than that known for northern populations, but a more accurate hypothesis might be that the breeding period in northeastern Mexico is protracted because the earliest observation of pairing occurred in late April (Knopf and Rupert 1999a) and the latest nest with eggs was observed in early July.

Vegetation characteristics near the nest we found corresponded with those reported by Graul (1975; height <8 cm), Knopf and Miller (1994; bare ground ≥30%), and Desmond and Chavez-Ramirez (2002; height = 2.3 cm, bare ground = 86.4%). The presence of a shading element near the nest is considered important in nest-site selection (Graul 1975, Olson and Edge 1985, Knopf and Miller 1994); the nearest shade we found was 40 m from the nest (a cluster of *Atriplex* sp.). Dominant plant species differed from those reported in association with Mountain Plover nest sites: blue grama, buffalograss, needle-and-thread, and sagebrush (Finzel 1964, Graul 1975, Knowles et al. 1982). In Llano La Soledad, however, *Muhlenbergia* sp. and Karwinski's grama were the dominant grasses, and summer bluet and McVaugh's bladderpod were the dominant forbs; buffalograss occurs in the area but was not common (RD = 0.1, RF = 5.2; Table 1).

The presence of a disjunct Mountain Plover breeding population in northeastern Mexico—and its association with colonies of Mexican prairie dogs—has strong conservation implications for grasslands in that region. However, the last remnants of northeastern Mexico's native grasslands and Mexican prairie dog habitats are being lost, which could have negative effects on the region's population of Mountain Plovers. Other avian species that commonly occur in association with Mexican prairie dog colonies include Long-billed Curlew (*Numenius americanus*), Ferruginous Hawk (*Buteo regalis*), Burrowing Owl (*Athene cunicularia*), and an endemic, Worthen's Sparrow (*Spizella wortheni*); they, too, could be at risk of declines due to habitat loss.

ACKNOWLEDGMENTS

We thank F. L. Knopf, C. C. Farquhar, E. Iñigo-Elias, and two anonymous referees for their comments and suggestions on the manuscript.

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The Wilson Journal of Ornithology 118(1):85–90, 2006

BREEDING BIOLOGY OF THE DOUBLE-COLLARED SEEDEATER (*SPOROPHILA CAERULESCENS*)

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ABSTRACT.—The Double-collared Seedeater (*Sporophila caerulescens*) is the most common seedeater in southern South America. Because information on its breeding biology is mostly limited to descriptions of nests and eggs, I studied the reproductive biology of the Double-collared Seedeater in southeastern Brazil. I found 41 active nests during seven breeding seasons (1997–2003). Nesting occurred from December to May. All nests found during incubation contained two eggs, eggs were laid on consecutive days, and incubation started the morning the female laid the last egg. Incubation and nestling periods were 12 and 12–15 days, respectively. Only females incubated the eggs. Mean time spent incubating/hr was 52.3 min, and incubation recesses averaged 6.6 min. Nestlings were fed 7.6 times/hr, and although both males and females fed the young, the participation of females was significantly greater than that of males. Predation was the major cause of nest failure. Daily survival rates during the incubation (0.990) and nestling (0.935) stages differed. Overall nesting success was 36%. Although studies conducted in disturbed areas can reveal greater rates of nest predation than those found in undisturbed areas, some *Sporophila* species seem to benefit from habitat disturbance. The conversion of native habitats to agricultural lands in Brazil, as well as the spread of exotic grasses, has resulted in the expansion of the Double-collared Seedeater to previously forested areas. *Received 14 February 2005, accepted 16 November 2005.*

The genus *Sporophila* (Emberizidae) comprises a diverse group of small finches widely distributed in the Neotropics. The greatest diversity is reached in interior South America, where most species inhabit grassy semi-open areas (Ridgely and Tudor 1994, Sick 1997). However, detailed information on breeding biology is lacking for most of these species. Furthermore, the melodious songs of these seedeaters make them vulnerable to pursuit for the illegal pet trade. As a result, many species have been locally extirpated, and some are severely threatened (Collar et al. 1992, Willis and Oniki 1992, Ridgely and Tudor 1994, Sick 1997, Willis 2003).

The Double-collared Seedeater (*S. caerulescens*) is the most common seedeater in southern South America. It inhabits grasslands and agricultural areas (Ridgely and Tudor 1994), commonly near populated locations. Recently, it has expanded its distribution in response to the destruction of forested areas and the consequent spread of exotic grass species (Sick 1997). Although not endangered, entire populations of the Double-collared Seedeater have been lost to the illegal pet trade, being one of the most popular cage birds in Brazil. Information on its breeding biology is limited to descriptions of nests and eggs (Euler 1900, Ihering 1900, Pereyra 1956, De La Peña 1981, Alabarce 1987) and the length of the nestling period—obtained from a single nest observed in Argentina (Pereyra 1956). More information on the species' ecology is needed before meaningful conservation objectives can be developed for the species. Herein, I describe the reproductive biology of the Double-collared Seedeater in southeastern Brazil. Phenology and duration of the breeding season, length of incubation and nestling periods, egg mass, nest success, and information on parental care are reported.

METHODS

Study area.—I conducted my study on the campus of São Carlos Federal University, located in the central region of São Paulo state, southeastern Brazil (21° 58′ S, 47° 52′ W). The campus is subdivided into a semi-urbanized portion and an adjacent non-urbanized, disturbed *cerrado* area (savanna that ranges from open grasslands to forested areas, such as gallery forests that grow alongside watercourses; Eiten 1972). The semi-urbanized area totals 187 ha, and is composed of extensive lawns, orchards, gardens, and *Eucalyptus* spp. and *Pinus* spp., with regenerating *cerrado* undergrowth. Buildings and streets are widely spaced and compose only 23 ha (12%). The

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non-urbanized area is a 529.6-ha mosaic composed of *sensu lato cerrado* (125 ha), gallery forest (3.6 ha), regenerating *cerrado* (84 ha), an abandoned *Eucalyptus* spp. plantation with regenerating *cerrado* undergrowth (94 ha), and active *Eucalyptus* spp. silviculture (223 ha) (Paese 1997). The climate in this region is tropical, with two well-marked seasons: a humid, hot season from October through March and a dry, cold season from April through September. In both the semi-urbanized and non-urbanized areas, grass seeds are abundant during the wet season.

During seven breeding seasons (1997–2003), I conducted nest searches from early November, when males started to sing and defend territories, to May, when males stopped singing. All habitats were searched for nests. Although I conducted nest searches weekly, the number of habitats covered and search effort varied on each field survey. Nests were located by searching the areas defended by males and by following females observed near these territories. Using a metal caliper (accurate to 0.01 mm), I measured nests and eggs, and I used a spring scale (accurate to 0.1 g) to weigh eggs.

Using a 7 × 35 binocular, I observed nests during 60-min periods to calculate the frequency of feeding visits and to estimate the proportion of time that females spent incubating the eggs. These observations were always made early in the morning (06:00–10:00 UTC−3) and while maintaining a minimum distance of 20 m from the nests. During the nestling stage, only nests containing two young (the most frequent brood size) were considered for observations. The nestling stage was subdivided into three observation periods: early (1–4 days after hatching), middle (5–9 days after hatching), and late (10–13 days after hatching; Roper and Goldstein 1997). I used the Kruskal-Wallis test to compare the frequencies of feeding trips among these periods. To compare the number of times that males and females fed the young, I used the Mann-Whitney *U*-test.

I checked nests every 1–3 days. Predation was assumed to have occurred when eggs or nestlings younger than fledging age disappeared from a nest. Abandonment was assumed if adults were not seen on or near the nest and the eggs were cold or the nestlings were dead (Pletschet and Kelly 1990). Whenever possible, I checked nests from a distance. By using binoculars, I was able to see eggs and young through the thin nest walls, thus avoiding observer disturbance (see Roper and Goldstein 1997). I estimated rates of daily nest survival during the incubation and nestling stages by using the Mayfield method (Mayfield 1961), and compared them according to Sauer and Williams (1989) by using program CONTRAST (Hines and Sauer 1989). One to six nests of each stage were analyzed per year in order to calculate survival rate, but because of small sample sizes, years were pooled. Means of daily survival rate are presented ± SE; all other means are presented ± SD. I calculated standard errors according to Johnson (1979). Nesting success (probability of survival) from incubation through fledging was also estimated following Mayfield (1961).

RESULTS

I found 41 active nests, 26 in the semi-urban area and 15 in disturbed *cerrado*. Nests were found in all habitats except gallery forest and active *Eucalyptus* spp. plantations. Males started defending territories in early November, and I found the earliest nest on 18 December 1999. The nest contained two eggs in the late stage of incubation, suggesting that breeding activities had started in early December. The latest nesting activity was recorded on 9 May 1997, when I observed the last young in a nest.

Nests were cup-shaped and built of thin grass roots and spiderweb silk. The walls were thin, as the eggs and young could be seen through them. The eggs were white or slightly greenish, with dark and light brown spots, sometimes concentrated at the large end of the egg (Euler 1900, Ihering 1900, De La Peña 1981). The height of nests above ground ranged from 0.6 to 6 m (2.4 ± 1.2, $n = 25$). I also measured outside diameter (6.7 cm ± 0.8, $n = 19$), inside diameter (5.2 cm ± 0.7, $n = 19$), inside height (4.0 cm ± 0.6, $n = 18$), and outside height (4.8 cm ± 0.7, $n = 19$) of the nests. Egg measurements were length = 17.7 mm ± 0.5, $n = 11$; width = 13 mm ± 0.5, $n = 11$; and weight = 1.4 g ± 0.5, $n = 11$.

Double-collared Seedeaters did not appear to select any particular plant species for nest construction. Eighteen species belonging to 11 different families were identified, including the exotic *Pinus* spp. (Pinaceae), *Cupressus* spp. (Cupressaceae), *Eriobotrya japonica* (Rosaceae), *Michelia champaca* (Magnoliaceae), *Ligustrum lucidum* (Oleaceae), *Murraya exotica*, *Citrus* sp. (Rutaceae), and *Eupatorium* sp. (Asteraceae). Native plant species included *Piptocarpha rotundifolia*, *Vernonia* sp. (Asteraceae), *Didymopanax vinosum* (Araliaceae), *Miconia albicans*, *Tibouchina granulosa* (Melastomataceae), *Machaerium acutifolium*, *Caesalpinia peltophoroides*, *Sweetia elegans*, *Sibipiruna sibipiruna* (Fabaceae), and *Casearia silvestris* (Flacourtiaceae).

All nests observed during incubation contained two eggs ($n = 27$). Eggs were laid on consecutive days and incubation started the morning the female laid the last egg (first day of incubation). Hatching occurred on the morning of the 13th day ($n = 4$ nests). During 33 hr of focal observations at seven different nests, I observed only females incubating the eggs. Males did not feed females on the nests. The mean time spent incubating/hr was 52.3 min ± 5.8 (range = 41.2–60 min), and incubation recesses were 6.6 min ± 4.4 (range = 0.3–18.7 min, $n = 23$).

Nestlings fledged in 12–15 days (mean = 13.3 ± 1.2, $n = 8$), and invariably, nestlings from the same nest fledged on the same day ($n = 4$ nests). They left the nests with poorly developed feathers and weak flight capabilities. In 34 hr of focal observations at 11 different nests, nestlings were fed an average of 7.6 ± 4.3 times/hr. The number of feeding visits/hr increased throughout the nestling period (Fig. 1), and although both males and females fed the young, the participation of females (4.8 visits/hr ± 2.4) was significantly greater than that of males (2.7 ± 2.5; $U = 341.0$, $P = 0.001$).

Females regularly brooded nestlings after feedings (until the young were up to 7 days old), and both males and females removed fecal sacs. In one territory, adults fed one fledgling and young nestlings at the same time, suggesting that the nestlings represented at least a second brood for that breeding season. On several occasions, one or both adults of a pair were observed chasing intruding Double-collared Seedeaters that approached nests.

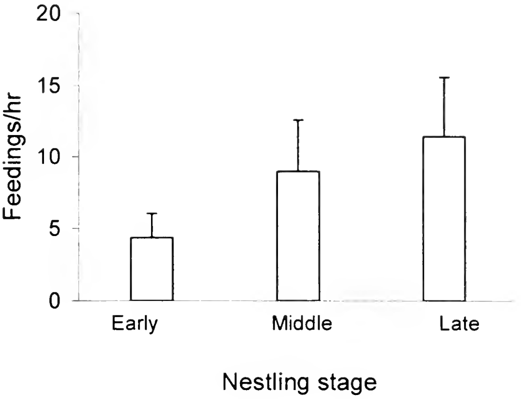

FIG. 1. Average number of feedings/hr in the early ($n = 14$ hr at eight different nests), middle ($n = 9$ hr at five different nests), and late ($n = 11$ hr at six different nests) nestling stages. Error bars are SDs. The frequency of feedings differed among the stages (Kruskal-Wallis $H = 16.38$, $P < 0.001$).

Apart from one nest that fell down during a storm, predation was the only cause of nest failure. No nests were abandoned and no eggs were infertile. Daily survival during incubation was 0.990 ± 0.010 (one predation event in 104 nest days, $n = 12$ nests). Survival during the nestling stage was 0.935 ± 0.024 (seven predation events in 107 nest days, $n = 13$ nests). Nest survival was higher during incubation (11 of 12) than during the nestling stage (6 of 13; $\chi^2 = 4.5$, df = 1, $P = 0.033$). Nesting success from incubation to fledging was 36%.

The mean number of female arrivals and departures from nests during the incubation stage was 1.9 ± 2.0/hr ($n = 33$ hr). During the nestling stage, the mean number of parental arrivals and departures was 15.7 ± 9.2 ($n = 34$ hr). The mean number of parental departures and arrivals per hr was greater during the nestling stage than it was during incubation ($U = 31.5$, $P < 0.001$).

DISCUSSION

The nesting season of Double-collared Seedeaters began in December, which is late compared with the onset of breeding season for most passerine birds inhabiting *cerrado* (i.e., they usually start in September; Sick 1997). Nesting in Double-collared Seedeaters coincided with the fruiting period of exotic Gramineae species, seeds of which are fed to nestlings. Entire seeds of *Brachiaria* sp. were observed in the crops of nestlings. Other seedeaters found in the study region, such as *S. lineola* and *S. leucoptera*, shared the same breeding period (MRF pers. obs.).

The nests were similar to those described for other *Sporophila* species (e.g., *S. collaris*, *S. ruficollis*, *S. albogularis*, *S. nigricollis*, and *S. lineola*; Alderton 1961; ffrench 1965; De La Peña 1981; Marcondes-Machado 1982, 1997), and the cup shape and thin walls were typical of those constructed by congeners (Sick 1997). The use of spiderwebs in nest construction has also been recorded for *S. ruficollis* (De La Peña 1981) and *S. nigricollis* (ffrench 1965). Nests were not reused, as previously reported for *S. nigricollis* (Alderton 1961), *S. albogularis*, and *S. lineola* (Marcondes-Machado 1982, 1997), but females reused the material of old nests to build new nests.

The incubation period of 12 days was similar to that of *S. nigricollis* and *S. americana* (it lasts 13 days for *S. torqueola*). For *S. caerulescens*, Pereyra (1956) reported a nestling period of 13–14 days, and I observed a mean of 13.25 days. The nestling period is 8–9 days for *S. nigricollis*, 11–13 days for *S. americana*, 11 days for *S. torqueola*, and 9 days for *S. lineola* (Skutch 1945, Gross 1952, Alderton 1961, Marcondes-Machado 1997). Overall, both the incubation and nestling periods reported for the *Sporophila* species are among the shortest of Neotropical, open-cup nesting Passeriformes. Although some nests of *S. americana*, *S. lineola* (Skutch 1945, Gross 1952, Marcondes-Machado 1997), and *S. caerulescens* (De La Peña 1981), have been found containing three eggs or young, two seems to be the usual brood size for *Sporophila* species.

Predation was by far the major factor limiting nesting success in *S. caerulescens*, similar to reports for many other open-cup nesting Neotropical passerines (Skutch 1949, 1985; Snow 1976; Oniki 1979; Roper and Goldstein 1997; Martin et al. 2000; Mezquida and Marone 2000). My data support the hypothesis that parental activity may increase the risk of nest predation (Skutch 1949, 1985). The number of adult departures from, and arrivals to, nests were much greater, and daily survival was lower during the nestling stage. Skutch's hypothesis predicts that the primary predators should be diurnal and visually oriented. However, in addition to parental activities, nests containing nestlings may be more conspicuous due to the noise (Haskell 1994, 1999; Dearborn 1999) and odor of the young, which would attract nocturnal mammalian predators that use olfaction. Nestlings vocalized only when parents were feeding them, and the begging calls were audible from 15 m when broods were 7–8 days old, and from about 20 m when young were in the late nestling stage.

Although little is known about nest predators in the Neotropics, preliminary observations and video data have shown diurnal birds to be the most important predators in environments other than wet forests (Martin et al. 2000, Mezquida and Marone 2002). Potential predators in the study area included Burrowing Owl (*Athene cunicularia*; Mezquida and Marone 2000), Guira Cuckoo (*Guira guira*; Mason 1985), Squirrel Cuckoo (*Piaya cayana*), and anis (*Crotophaga* spp.; Telleria and Diaz 1995). During my study, I observed a Great Kiskadee (*Pitangus sulphuratus*) preying upon a Double-collared Seedeater nest. I have also observed Plush-crested Jays (*Cyanocorax chrysops*) feeding on Common Quail (*Coturnix coturnix*) eggs placed in artificial cup-shaped nests (MRF unpubl. data), which suggests their potential as a predator of seedeaters, as well. Potential nocturnal mammalian predators occurring in the study area included white-eared opossum (*Didelphis albiventris*), crab-eating raccoon (*Procyon cancrivorus*), grison (*Galictis vittata*), striped hog-nosed skunk (*Conepatus semistriatus*), tayra (*Eira barbara*), jaguarundi (*Herpailurus yaguarondi*), and house cats (*Felis catus*).

Studies conducted in disturbed areas can reveal greater rates of nest predation than those in undisturbed areas due to the increased abundance of mesopredators in disturbed areas (Martin 1996, Martin et al. 2000). However, some *Sporophila* species seem to benefit from habitat disturbance. Before its expansion into anthropogenic habitats, the niche occupied by the Double-collared Seedeater was probably limited to non-forested areas, such as forest borders, *cerrado*s, and wetlands where native grasses occurred. Today, the increasing extension of agricultural areas in Brazil, as well as the spread of exotic grasses, has resulted in the expansion of Double-collared Seedeaters to areas previously covered by forests. Gross (1952) and ffrench (1965) provide additional records of the expansion of *S. americana* and *S. nigricollis* into anthropogenic habitats.

ACKNOWLEDGMENTS

I am grateful to N. Arguedas, H. L. Gibbs, M. Rodrigues, M. A. Pizo, M. Galetti, and three anonymous referees for their important suggestions on previous versions of this manuscript, and M. I. S. Lima for identifying plant species. This study was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP).

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The Wilson Journal of Ornithology 118(1):91–98, 2006

SMALL MAMMAL SELECTION BY THE WHITE-TAILED HAWK IN SOUTHEASTERN BRAZIL

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ABSTRACT.—We analyzed diet and prey selection of the relatively unknown *albicaudatus* subspecies of the White-tailed Hawk (*Buteo albicaudatus*). Our study was based on an analysis of 259 pellets collected from September 2000 to September 2001 in the municipality of Juiz de Fora in southeastern Brazil. We also assessed the abundance of small mammals with pitfall traps (2,160 trap-nights). Small mammals composed 52.5% of the estimated biomass consumed by the hawks, and selection appeared to be mediated by abundance. The Bonferroni confidence intervals procedure revealed that when abundance of small mammals was higher, the hawks were selective, preying on *Calomys tener* more than would be expected by chance ($P < 0.05$); other rodents were consumed less than expected. *Oligoryzomys nigripes*, *Oxymycterus* sp., and *Gracilinanus* spp. were taken in the same proportion as they were found in the field. During reduced prey abundance (October–March), White-tailed Hawks preyed opportunistically on small mammals. Differences in habits and vulnerability of small mammals may explain prey selectivity in the White-tailed Hawk. *Received 5 October 2004, accepted 3 October 2005.*

The White-tailed Hawk (*Buteo albicaudatus*) is a poorly known species ranging from southern Texas to northern Argentinean Patagonia (Farquhar 1992, Thiollay 1994). Information on its ecology is scarce and largely descriptive or anecdotal, with most studies having been conducted in North America (Stevenson and Meitzen 1946, Kopeny 1988, Farquhar 1992). Data on type and number of prey have received some attention in Texas (see Farquhar 1992), but prey selection relative to prey abundance remains unknown. Only three studies report on the diet of this raptor in the Neotropics. Schubart et al. (1965) examined contents of two stomachs containing mainly insects; Brasileiro et al. (2003) reported predation on a snake, and Motta-Junior and Granzinolli (2004) observed consumption of a Ringed Kingfisher (*Megaceryle torquata*). The species is thought to be an opportunistic predator (Stevenson and Meitzen 1946, Kopeny 1988), and in Texas, half of the prey biomass comprises mammals (Farquhar 1986).

Opportunistic predators generally take prey in accordance with their abundance in the field, whereas selective predators consume prey in proportions that differ from those available (Jaksic 1989). This selectivity or opportunism may be explained in relation to the energy costs and benefits involved in the capture and handling of prey. Predators may consume the most profitable, but not necessarily the most abundant, prey (Schoener 1971, Korpimäki 1985, Stephens and Krebs 1986, Iriarte et al. 1989, Jaksic 1989). According to optimal foraging theory, predators behave to maximize their fitness, which is done by maximizing their net rate of energy intake (Emlen 1966, 1968; Schoener 1971; Stephens and Krebs 1986). Thus, prey selection by a predator not only depends on prey energy content, but also on the predator's success in three basic stages: finding, handling, and consuming prey. Selectivity can be assessed by observing differences among the prey species at any of these steps. Prey selectivity may be a result of both prey and predator morphology and behavior (Corley et al. 1995). Emlen (1966, 1968) hypothesized that predators will exhibit a greater degree of dietary selection when their prey are abundant, but will be more opportunistic when food is scarce. Additionally, a predator may eat more abundant prey at greater frequencies than expected in relation to abundance (Emlen 1966). Here, we analyze prey selection by the White-tailed Hawk relative to prey abundance, evaluating previous assertions about the opportunistic feeding behavior of this species (Stevenson and Meitzen 1946, Farquhar 1986, Kopeny 1988).

METHODS

Study site.—We conducted fieldwork on private farmlands in northern Juiz de Fora (21° 41′ S, 43° 27′ W), in the state of Minas Gerais

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in southeastern Brazil (Fig. 1). The elevation of our study area (17,537 ha) ranged from 670 to 800 m; the topography is mountainous. The climate is Humid Subtropical, winters are dry, and annual rainfall averages 1,536 mm. The wet season extends from October to April (192 mm rainfall, mean temperature = 20.2° C), and the dry season occurs from May to September (37 mm rainfall, mean temperature = 16.8° C). Originally, the dominant vegetation was semi-deciduous forest; now the area is primarily farmland, pastures, patches of second-growth vegetation, and plantations of exotics (e.g., *Eucalyptus* spp. and *Pinus* spp.; Juiz de Fora 1996).

General diet.—The analysis of the White-tailed Hawk's diet was based on 259 pellets, which we collected from seven nesting and six roosting sites of approximately seven pairs. We collected and identified (by size and shape) all pellets from perches used exclusively by White-tailed Hawks. We oven-dried the collected material and treated it with a 10% NaOH aqueous solution (Marti 1987). Prior to chemical treatment, we removed remains of scales, fur, and feathers, and later added them to other remains, such as mandibles, teeth, and invertebrate exoskeletons. We identified remains by comparing them to a reference collection from the study area. Invertebrates were generally identified to family and order, whereas vertebrates were identified mostly to genus or species. Prey biomass was estimated by counting the minimum number of individuals in pellets and then multiplying this number by the mean body mass of each species at the study site (Marti 1987).

Prey selection.—We estimated the relative abundance of small mammals in the field by monitoring five sets of drift-fence pitfall traps (Friend et al. 1989). Traps were distributed systematically around most of the hawks' hunting sites (Fig. 1), determined before and during the study period through observations of foraging individuals. We collected pellets during small mammal trapping. Each set of pitfall traps consisted of 12 buckets (36 l each), totaling 60 traps. From September 2000 to September 2001, we operated traps monthly for 3 consecutive days, totaling 2,160 trap-nights. Captured mammals were identified, weighed, sexed, earmarked, and released. An index of small mammal abundance for each month was based on the total number of individual first captures (recaptures were not counted).

Indices of prey abundance are assumed to reflect prey availability, but this may not necessarily be true (Jaksic 1989). Traps should be efficient, nonselective, and catch the entire range of small mammal prey. Moreover, traps should be placed in patches where and when the predator hunts. Our procedures fulfilled these assumptions, in terms of both time and place of foraging. Our traps were open 24 hr per day, so that both diurnal and crepuscular activities of White-tailed Hawks were accounted for by the trapping procedures. Pitfall traps appear to be less selective and more efficient, capturing larger numbers of species, individuals, and age classes compared with traditional live traps (Williams and Braun 1983; MAMG unpubl. data).

Analyses.—We conducted *G*-tests to test the goodness-of-fit of the frequency distributions of prey in the diet and in the field (Zar 1984). We interpreted nonsignificant results to mean that White-tailed Hawks exploited prey in proportion to their abundance in the field; significant differences suggested that the hawks "preferred" or "avoided" some small mammal species, hence apparently selecting or avoiding prey. To confirm selection or avoidance of prey, we used the Bonferroni confidence intervals procedure for each prey species (Neu et al. 1974, Byers et al. 1984, Plumpton and Lutz 1993, Martinez and Jaksic 1997, McLoughlin et al. 2002). If the expected proportion of consumption was not included in the confidence interval, then the observed and expected consumption differed significantly. If the confidence interval included the expected proportion of consumption, then the hypothesis that prey species were preferred or avoided was rejected. All tests were considered significant at $P < 0.05$.

RESULTS AND DISCUSSION

General diet.—Numerically, the main prey were insects, followed by small mammals, reptiles, and birds (Fig. 2). Small mammals composed the bulk of biomass, followed by insects, reptiles, and birds. Our results are similar to those of Stevenson and Meitzen (1946), Farquhar (1986), and Kopeny (1988).

Only 5 of 12 genera of small mammals

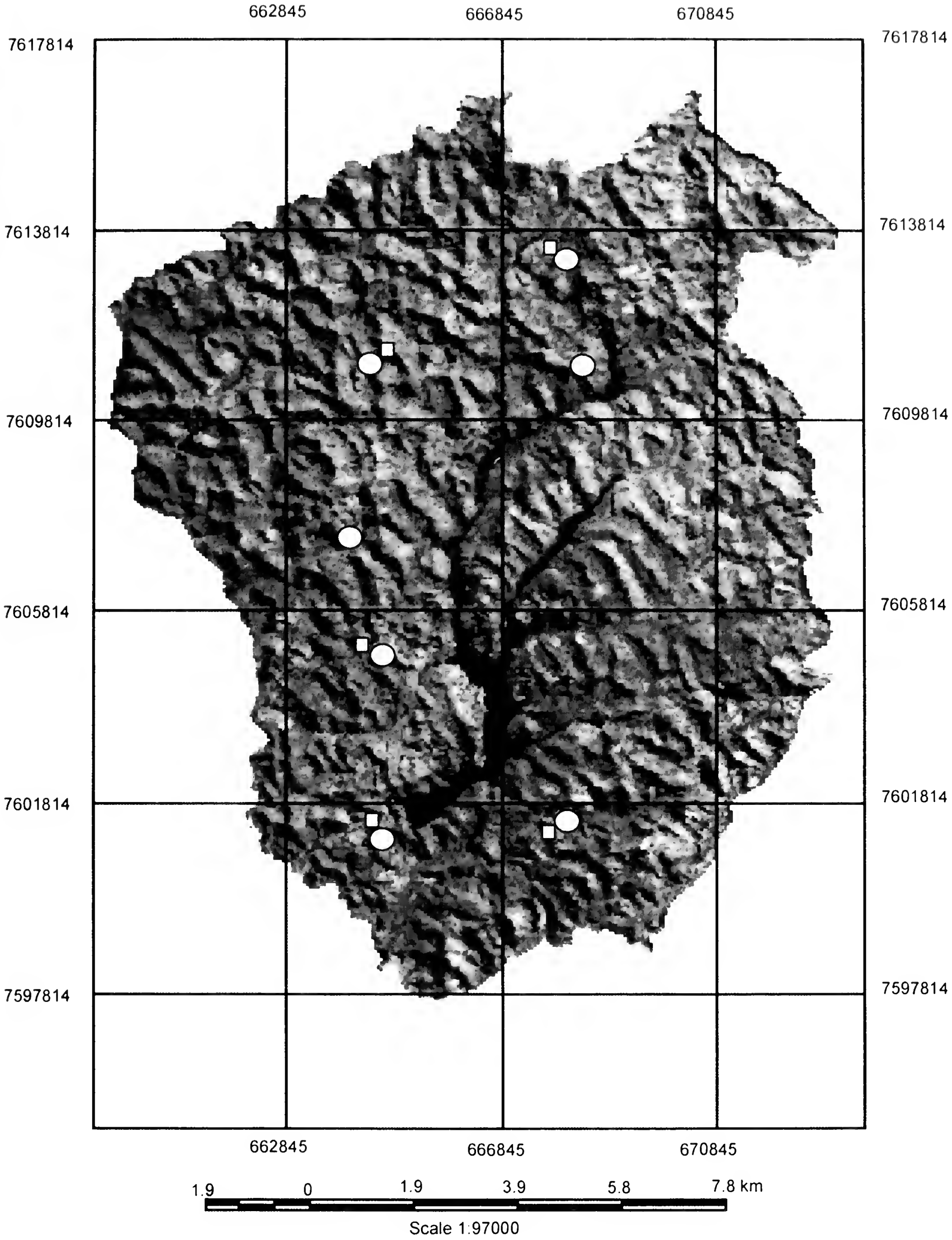

FIG. 1. Satellite image (LANDSAT 7/ETM, 27 June 2000) of study area in Juiz de Fora municipality, Minas Gerais, southeastern Brazil. Coordinate grid system is UTM (Zone 22, Corrego Alegre). White squares are sites of pitfall traps; white circles are nest and perch sites of White-tailed Hawks.

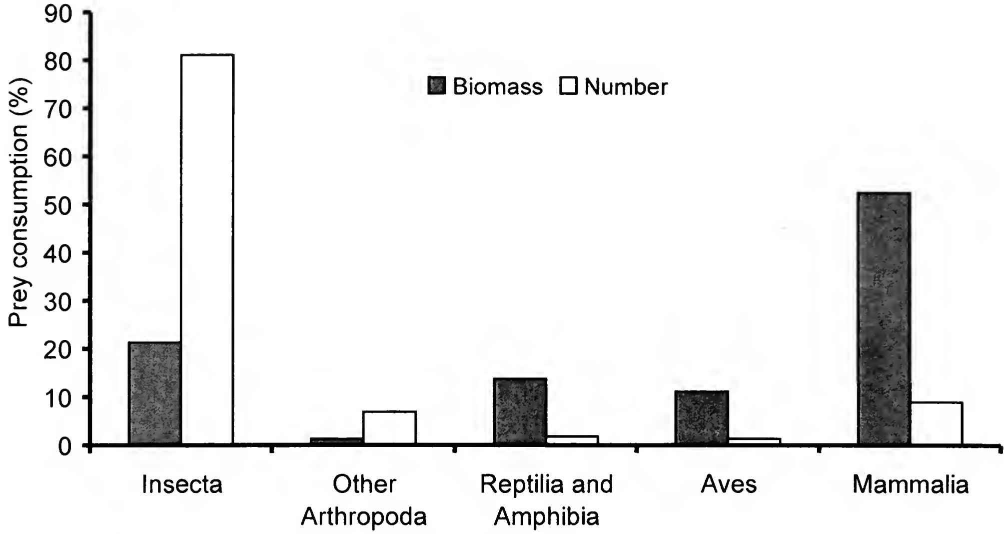

FIG. 2. Number of individuals and estimated biomass of prey groups consumed by White-tailed Hawks from September 2000 to September 2001, Juiz de Fora municipality, Minas Gerais, southeastern Brazil.

(*Calomys*, *Akodon*, *Oligoryzomys*, *Oxymycterus*, *Gracilinanus*) found in the study area (Appendix) were identified in White-tailed Hawk pellets. The genus *Akodon* was represented mostly by *A. lindberghi*, with some *A. cursor*; both were found in pellets and in pitfall traps. The seven genera whose remains were not found in pellets were uncommon: only 12 individuals (4.6% of total captures) were trapped in pitfalls (Appendix). Prey behavior or habitat choice may explain the absence of some genera in the diet of White-tailed Hawks. *Rhagomys*, *Oryzomys*, and *Juliomys* (=*Wilfredomys*) have arboreal or scansorial habits, whereas *Thaptomys*, *Bibimys*, *Bolomys*, and *Blarinomys* display subterranean or fossorial habits, and all but *Bolomys* and *A. lindberghi* inhabit mostly forests (Emmons 1990, Eisenberg and Redford 1999, Nowak 1999; JCM-J pers. obs.). Furthermore, although the genus *Oxymycterus* was as uncommon as the seven genera not recorded in White-tailed Hawk pellets, its habitat is mostly open vegetation (MAMG unpubl. data).

Prey selection.—White-tailed Hawks exhibited differential predation on small mammal species when both seasons were combined ($G = 32.54$, $P < 0.001$; Table 1). The same pat-

TABLE 1. Small mammal prey selection by White-tailed Hawks in Juiz de Fora municipality, Minas Gerais, southeastern Brazil, from September 2000 to September 2001. Observed values (Obs) are actual frequencies in the diet; expected values (Exp) are frequencies calculated from proportions obtained in the field by pitfall trapping.

	Dry season		Wet season		Total diet	
Species	Obs	Exp	Obs	Exp	Obs	Exp
Akodon spp.	11	33.5	6	7.5	17	40.8
Calomys tener	95	59.1	18	23.7	113	83.1
Oligoryzomys nigripes	24	41.3	14	6.8	38	47.9
Oxymycterus sp.[a]	2	0.7	1	—	3	0.7
Gracilinanus spp.[a]	4	1.4	1	2.0	5	3.5
Total	136	136.0	40	40.0	176	176.0
G[b]	52.07		7.68		32.54	
P	<0.001		0.054		<0.001	

[a] *Oxymycterus* sp. and *Gracilinanus* spp. were grouped for *G*-tests.
[b] *G*-test, df = 3.

tern was observed during the dry season ($G = 52.07$, $P < 0.001$), but not in the wet months ($G = 7.68$, $P = 0.054$; Table 1).

The Bonferroni confidence intervals procedure revealed that in the dry season, the hawks preyed more on *Calomys tener* and less on *Akodon* spp. than expected based on trapping data (Table 2). Conversely, in wet months, there were no differences in small mammal predation compared with the availability of small mammals in the study area (Table 2). *Oligoryzomys nigripes*, *Oxymycterus* sp., and *Gracilinanus* spp. were always consumed in the same proportion that they were found in the environment (Table 2). Hence, our findings are not entirely congruent with those of Stevenson and Meitzen (1946) and Kopeny (1988).

Other studies on small mammal populations in southeastern Brazil indicate peaks of abundance during the dry season (e.g., Motta-Junior 1996, Vieira 1997, Talamoni and Dias 1999). The same pattern was observed in our study (Fig. 3).

The high frequency of *C. tener* (sometimes considered a subspecies of *C. laucha*; Eisenberg and Redford 1999) in the White-tailed Hawk's diet may be due to its higher vulnerability. A similar suggestion was proposed by Corley et al. (1995) for other rodent and predator species in Patagonia. A less vulnerable species (*Eligmodontia typus*, better escape ability) was preyed upon less than expected by the culpeo fox (*Dusicyon culpaeus*), while the behaviorally and morphologically vulnerable *Akodon* spp. were consumed more frequently than expected. Other diet studies of owls (Motta-Junior 1996, Motta-Junior and Bueno 2004, Motta-Junior et al. 2004) in southeastern Brazil have revealed that *C. tener* is one of the main prey species, despite not being the most abundant in the field, suggesting higher vulnerability. *C. tener* is apparently mainly terrestrial and does not dig burrows (Eisenberg and Redford 1999, Nowak 1999); thus, it is more vulnerable because it is likely to be more conspicuous to the hawks. In contrast, species of *Akodon* travel in tunnels under the leaf litter and nest in burrows (Emmons 1990); thus, *Akodon* spp. may be able to escape White-tailed Hawk predation more efficiently than *C. tener*.

Our results suggest that prey selection by

TABLE 2. Bonferroni confidence intervals analysis for small mammal selection (usage) by White-tailed Hawks during the dry and wet seasons from September 2000 to September 2001, Juiz de Fora municipality, Minas Gerais, southeastern Brazil. If the expected proportion of usage (P_{io}) was greater than the upper confidence interval estimate, the prey species was consumed less than expected (−). Conversely, a P_{io} lower than the lower confidence interval estimate suggests that the prey species was exploited more than expected (+). If an expected proportion fell within the confidence interval, prey consumption was similar to prey availability (0).

	Dry season			Wet season		
Species	Actual proportion of usage (P_i)	Expected proportion of usage (P_{io})	Bonferroni intervals for P_i	Actual proportion of usage (P_i)	Expected proportion of usage (P_{io})	Bonferroni intervals for P_i
Akodon spp.	0.081	0.304	$0.020 \leq p_i \leq 0.141$ (−)	0.150	0.187	$0.004 \leq p_i \leq 0.295$ (0)
Calomys tener	0.699	0.435	$0.597 \leq p_i \leq 0.799$ (+)	0.450	0.593	$0.247 \leq p_i \leq 0.652$ (0)
Oligoryzomys nigripes	0.176	0.246	$0.092 \leq p_i \leq 0.260$ (0)	0.350	0.170	$0.155 \leq p_i \leq 0.544$ (0)
Oxymycterus sp.	0.015	0.005	$0.000 \leq p_i \leq 0.041$ (0)	0.025	0.000	$0.000 \leq p_i \leq 0.088$ (0)
Gracilinanus spp.	0.029	0.010	$0.000 \leq p_i \leq 0.066$ (0)	0.025	0.050	$0.000 \leq p_i \leq 0.088$ (0)

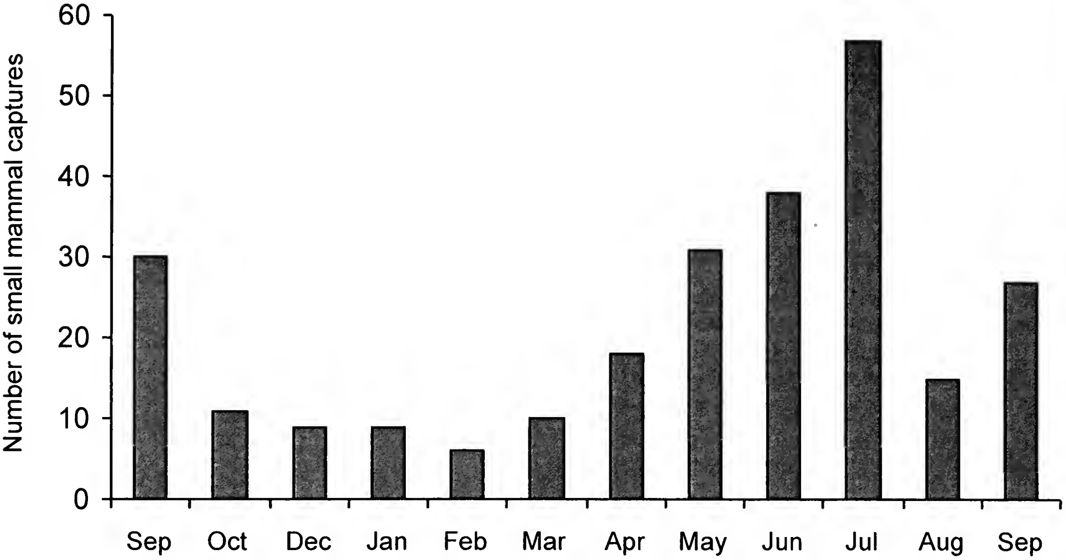

FIG. 3. Small mammal abundance from September 2000 to September 2001, Juiz de Fora municipality, Minas Gerais, southeastern Brazil. Data were not available for November 2000.

White-tailed Hawks was mediated by prey abundance. When the abundance of small mammals was higher (dry season), the hawks selected the more abundant prey, *Calomys tener* (Table 2). However, during a period of lower abundance of prey (wet season), White-tailed Hawks were opportunistic relative to small mammal species. Our results support the prediction of Emlen (1966) that predators feed selectively on very abundant prey, thus suggesting that White-tailed Hawks exploit resources depending on their availability.

In conclusion, White-tailed Hawks seem to prey selectively on a more vulnerable small mammal (*C. tener*), which has terrestrial habits and uses open habitat. The semi-fossorial *Akodon* spp. were apparently less vulnerable to the hawks. Alternatively, but not exclusively, our results support Emlen's (1966) hypothesis that predators, in times of high prey abundance, will prey selectively on species that are more abundant. Further studies of raptor diet selection in the Neotropics should stress morphological and behavioral traits of prey as a way to understand differential vulnerability to predators (e.g., Kotler 1985, Corley et al. 1995).

ACKNOWLEDGMENTS

We thank C. V. Rios for assistance in the field. M. V. Vieira, R. P. Kavanagh, C. C. Farquhar, A. A. Bueno, and two anonymous referees provided helpful comments on previous versions of our manuscript. Financial support was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico and the Fundação de Amparo a Pesquisa do Estado de São Paulo.

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APPENDIX. Rodents and opossums (*Gracilinanus* spp.) captured in pitfall traps in Juiz de Fora municipality, Minas Gerais, southeastern Brazil, from September 2000 to September 2001. For each month, we tallied only first captures. Data were not available for November 2000.

Species	Mean body weight (g)	Month												Total
		Sep	Oct	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	
Akodon cursor[a]	17	1	—[b]	—	1	—	1	1	2	—	—	—	—	6
Akodon lindberghi[a]	13	—	3	2	—	—	2	1	10	7	14	4	9	52
Bibimys labiosus	19	—	—	1	—	—	—	—	1	—	—	—	—	2
Blarinomys breviceps	12	—	—	—	1	—	—	—	—	—	—	—	—	1
Bolomys lasiurus	24	—	—	1	—	—	—	—	—	—	—	—	—	1
Calomys tener[a]	12	22	6	3	5	5	5	11	12	17	24	2	6	118
Gracilinanus agilis[a]	20	1	—	1	—	—	—	—	—	1	—	—	—	3
Gracilinanus spp.[a]	19	—	1	—	1	—	—	—	—	—	—	—	—	2
Juliomys sp.	20	—	—	—	—	—	—	—	—	—	—	—	1	1
Oligoryzomys cf. *flavescens*	18	1	—	—	—	—	—	—	—	—	—	—	—	1
Oligoryzomys nigripes[a]	11	4	1	1	1	1	1	5	6	13	18	6	10	67
Oryzomys cf. *kelloggi*	29	—	—	—	—	—	—	—	—	—	—	2	1	3
Oxymycterus sp.[a]	73	1	—	—	—	—	—	—	—	—	—	—	—	1
Thaptomys nigrita	22	—	—	—	—	—	1	—	—	—	—	—	—	1
Rhagomys rufescens	27	—	—	—	—	—	—	—	—	—	1	1	—	2
Total		30	11	9	9	6	10	18	31	38	57	15	27	261

[a] Species preyed on by White-tailed Hawks.

[b] — represents no captures.

Short Communications

The Wilson Journal of Ornithology 118(1):99–101, 2006

Provisioning of Fledgling Conspecifics by Males of the Brood-parasitic Cuckoos *Chrysococcyx klaas* and *C. caprius*

Irby J. Lovette,[1,4] Dustin R. Rubenstein,[1,2,3] and Wilson Nderitu Watetu[3]

ABSTRACT.—Although post-fledging care by adult males seems unlikely in bird species that are obligate, interspecific brood parasites, there have been numerous reports of adult male *Chrysococcyx* cuckoos apparently feeding conspecific young. Most researchers currently view these observations with skepticism, in large part because *Chrysococcyx* and other cuckoo species engage in courtship feeding, and it is possible that field observers could mistake adult females receiving food from courting males for fledglings, especially given the similar appearances of females and juveniles. Here, we report an observation of an extended provisioning bout by an adult male Klaas's Cuckoo (*C. klaas*) feeding a conspecific individual with juvenile plumage and behavior, and we summarize our observations of similar occurrences in the Diederik Cuckoo (*C. caprius*) in Kenya. We suggest that the available evidence indicates that male provisioning, and hence potential parental care, is present in these brood-parasitic cuckoos at a higher frequency than currently recognized. The mechanism that causes males to associate with fledglings is unknown, but warrants further study.

Received 20 December 2004, accepted 19 September 2005.

The genus *Chrysococcyx* comprises 15 species of small, Old World cuckoos (Sibley and Monroe 1990), of which all are thought to be obligate brood parasites (Davies 2000). Klaas's Cuckoo (*C. klaas*) has a wide distribution in sub-Saharan Africa, where it is known to parasitize a large number of passerine host taxa, often—but not exclusively—species of Sylviidae and Nectarinidae (Irwin 1988). Similarly, the Diederik Cuckoo (*C. caprius*) breeds throughout much of sub-Saharan Africa and has a broad range of hosts, primarily species of Ploceidae (Irwin 1988).

Over the past century, there have been numerous observations of male *Chrysococcyx* cuckoos feeding conspecifics that were thought to be fledglings (Moreau 1944, Friedmann 1968, Iversen and Hill 1983, Rowan 1983). In a literature review of provisioning behavior in brood parasites, Lorenzana and Sealy (1998) found 5 records of nestling or fledgling provisioning by Klaas's Cuckoo males and 11 such records for Diederik Cuckoo males; Friedmann (1968) discusses 12 and 15 such records, respectively, including some anecdotal reports. There is apparently only one equivalent report of a female *Chrysococcyx* cuckoo provisioning fledglings, and in that case, both the female and young were captive birds (Millar 1926, Lorenzana and Sealy 1998). Historically, a number of researchers (e.g., Moreau 1944, Friedmann 1968) considered parental care to be common in African *Chrysococcyx* cuckoos and believed that the behavior might be a primitive condition associated with a relatively recent evolutionary transition to brood parasitism. As researchers continued to document the prevalence of courtship feeding in these and other cuckoo species, more recent authorities (e.g., Rowan 1983, Irwin 1988, Lorenzana and Sealy 1998, Davies 2000) have suggested that the behavior is either misdirected courtship feeding or the result of human observers misidentifying adult females as fledglings. In practice, these and other possibilities are difficult to exclude. Although the plumages of adult African *Chrysococcyx* are highly sexually dimorphic, it is difficult to distinguish females from juveniles in the field (Rowan 1983).

Here, we report an observation of an extended provisioning bout by an adult male Klaas's Cuckoo feeding a conspecific individual with juvenal plumage and behavior, and we summarize our observations of similar occurrences in the Diederik Cuckoo. These ob-

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servations add to the body of evidence suggesting that male *Chrysococcyx* cuckoos may engage in intensive provisioning of juveniles.

KLAAS'S CUCKOO

Beginning at 10:08 UTC+3 on 15 August 2004, IJL, DRR, and WNW observed an adult male (by plumage) Klaas's Cuckoo in Lake Nakuru National Park, Kenya (00° 22′ S, 36° 03′ E). This bird was foraging at an extremely rapid rate of movement in the open canopy of a large yellow-barked acacia tree (*Acacia xanthophloea*). After watching the bird for a few minutes, we observed it deliver food to a second, sedentary cuckoo in the same tree. We noted the time, and for the next 26 min, we were able to keep both cuckoos under constant focal observation with at least one observer following each bird. This is apparently the longest-duration period of potential fledgling provisioning reported for *Chrysococcyx* (Friedmann 1968).

During our observation, the adult male cuckoo continued to forage rapidly within an approximate 40-m radius around the second cuckoo. The male returned to the second cuckoo 18 times while carrying food items, all of which appeared to be 1- to 3-cm-long lepidopteran larvae gleaned from the foliage and bark of the acacia. On 16 of the 18 visits, the second, more sedentary bird accepted and ate the caterpillar. On each visit, the adult male presented the food with his tail slightly cocked, but we observed no other conspicuous postures or behaviors potentially related to courtship. No copulations or attempted copulations occurred.

During our observation, the presumed juvenile moved among four perches, flying 3–4 m each time. These flights were notably more fluttery than those of the adult male and appeared typical of the weak flight exhibited by recently fledged birds. While perched, this bird also assumed the "fluffed" posture typical of recent fledglings, and it remained stationary between most provisioning visits. The observation ended when the presumed juvenile made a similar, but slightly longer flight into denser foliage and disappeared from our sight. Although the plumages of female and immature Klaas's Cuckoos are variable and overlap (Irwin 1988), we noted at the time that the bird being provisioned had a distinct white patch behind the eye and a white throat marked with substantial, dark barring—plumage characters more typical of juveniles (Irwin 1988).

DIEDERIK CUCKOO

On 28 May 2002 at 08:23, WNW observed a male Diederik Cuckoo feeding an apparent fledgling (based on plumage) at the Mpala Research Centre, Laikipia, Kenya (00° 17′ N, 36° 54′ E). The fledgling was perched about 3 m above ground in a *Balanites aegyptica* tree. During 15 min of observation, the adult fed the fledgling at least four times and continued to do so when the observer left the area. On 19 May 2003 at 10:15, WNW noted similar behavior at a site 100 m from that of the first observation. During this observation, an adult male Diederik Cuckoo gleaned insects from long grass and fed them to a fledgling (based on plumage) perched on a nearby acacia. We observed the male make six feeding trips before cattle flushed the birds.

DISCUSSION

Based on the posture, behavior, and plumage of the Klaas's Cuckoo that we observed being fed by an adult male, it seems highly likely that it was a recently fledged bird rather than an adult female being courted. We also noted that the adult male engaged in intensive (and, presumably, energetically costly) foraging for an extended period in order to provision this individual. Friedmann (1968) considered provisioning bouts as long as 15 min as "suggestive of the fact that the catering adult was not merely indulging in courtship feeding." Our observation of an intensive provisioning period of nearly twice that duration further supports this interpretation. In contrast, courtship feeding in *Chrysococcyx* typically involves a series of stereotyped behaviors that we did not observe: the male's presentation of food while simultaneously cocking his head and vibrating his wings and tail, postural bowing movements by the male, vocalizations by the male or both individuals, or (in some cases) subsequent copulation (Irwin 1988).

When considered in concert, our observations and those in dozens of previous reports describing equivalent behaviors suggest that males of several African *Chrysococcyx* cuckoos may provision fledglings regularly. Post-fledging associations of adults and offspring also have been documented in other brood-parasitic taxa, such as the Brown-headed Cowbird (*Molothrus ater*; Hahn and Fleischer 1995). Indeed, previous reports have documented male Klaas's and Diederik cuckoos provisioning both pre-volant young and multiple fledglings (Moreau 1944, Friedmann 1968, Lorenzana and Sealy 1998), thus excluding misidentification of adult females as sufficient explanation for this behavior. We speculate that not only are females sometimes misidentified as fledglings, but perhaps older fledglings being provisioned by males are sometimes mistaken for females being courted. If earlier reports were correct and provisioning of fledglings by adult males is relatively common in the African *Chrysococcyx*, it raises interesting questions about the genetic relatedness of the interacting individuals and their underlying social system.

ACKNOWLEDGMENTS

We thank M. Muchai and the many additional staff members of the Department of Ornithology, National Museums of Kenya who have greatly facilitated our field research in their country. We similarly acknowledge the Kenya Wildlife Service and the Mpala Research Centre for allowing us to conduct this research.

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The Wilson Journal of Ornithology 118(1):101–104, 2006

Widespread Cannibalism by Fledglings in a Nesting Colony of Black-crowned Night-Herons

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ABSTRACT.—I studied the diet and foraging behavior of fledgling Black-crowned Night-Herons (*Nycticorax nycticorax*) in a mixed-species nesting colony of Black-crowned Night-Herons and Snowy Egrets (*Egretta thula*) in New Orleans, Louisiana. In 1 of 5 years, cannibalism of nestlings that had fallen or climbed out of nests was common, accounting for 66 of 94 (70.2%) prey items taken by fledglings. Juveniles took younger conspecifics by both predation and scavenging. Isolated incidents of cannibalism among Black-crowned Night-Herons have been reported previously, but not on a colony-wide scale. *Received 2 December 2004, accepted 19 September 2005.*

Many researchers have studied the diets of adult and nestling Black-crowned Night-Herons (*Nycticorax nycticorax*; Bent 1926, Palmer 1962, Wolford and Boag 1971), but there are few data on the diet and foraging behavior of juveniles immediately after leaving the nest. Here, I provide the first report of wide-

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spread cannibalism and scavenging of conspecifics among fledglings in a nesting colony of Black-crowned Night-Herons.

METHODS

From 1 February to 18 July 2000, I monitored a colony of Black-crowned Night-Herons on Ochsner Island, Audubon Park, New Orleans, Louisiana (29° 56′ N, 90° 8′ W) as part of a long-term (1997–2001) study on reproductive success. Ochsner Island is a small (600 m^2) island in a man-made lagoon; the distance between the island and the shore of the mainland is approximately 6 m. The island's vegetation is dominated by Chinese tallowtree (*Sapium sebiferum*) and live oak (*Quercus* spp.). In 2000, 143 pairs of Black-crowned Night-Herons and 10 pairs of Snowy Egrets (*Egretta thula*) nested on the island. Nest height ranged from 1 to 7 m above ground. I recorded the diet and foraging behavior of approximately 70 juvenile night-herons from fledging until the end of the breeding season, when the members of the nesting colony dispersed. Night-herons were considered to have fledged when they left the nest permanently and were no longer fed by adults, at which point most were capable of clumsy flight. Prey items were identified by direct observation of foraging night-herons. Observations were made from the mainland, from which approximately half of the nests in the colony could be observed. I observed foraging juveniles for 546 hr.

RESULTS

Juvenile Black-crowned Night-Herons were fed by parents until 45 ± 3 (SD) days after hatching ($n = 23$). However, juveniles were able to climb out of the nest and onto surrounding vegetation as early as 30 days after hatching, returning to the nest when a parent approached with food. At 35 days, juveniles readily left their nests, often climbing out of the nest to solicit food from a nearby parent or unrelated adult night-heron.

Juveniles remained on the island for 1–3 weeks after leaving the nest permanently, forming small groups of one to four individuals from the same nest, or neighboring nests. Each group or lone individual occupied a small (7–9 m^2) territory on the ground and defended the area from passing adults and other fledglings (see Noble et al. 1938 for a full description of territoriality in juvenile night-herons). Fledglings rarely ventured into the water to hunt; rather, they spent most of their time foraging on the ground under active nests. Of 94 prey items that I saw juvenile night-herons consume, 66 (70.2%) were younger fledgling or nestling night-herons. I observed juveniles feeding on both chicks that they killed ($n = 20$) and chicks that were already dead when I began observations ($n = 46$). Other prey items included fish (10.6%), frogs (8.5%), brown rats (*Rattus norvegicus*; 4.3%), carrion dropped from active nests (3.2%), Wood Duck chicks (*Aix sponsa*; 2.1%), and a dead Snowy Egret nestling (1.1%).

Fledglings did not prey on chicks in nests or chicks perched in vegetation; they limited their attacks to nestlings on the ground that had fallen or climbed out of nests. Adults defended chicks in nests, but I never observed adults interfering with fledglings that were preying on chicks on the ground. Since older night-heron nestlings often left the nest to perch on nearby vegetation before fledging permanently, it was not always clear whether victims were nestlings that had fallen from nests or younger fledglings that had just left the nest. It is probable, however, that predation by fledgling night-herons increased mortality rates of chicks that had climbed out of the nest and would have otherwise been able to climb to safety. Older nestlings in low nests (<1.5 m above ground) often climbed out of the nest onto the ground before fledging, and were therefore more vulnerable to attacks than nestlings in high nests.

Small, weak, and moribund chicks were attacked more frequently than healthy-looking nestlings near the age of fledging. The victims were approximately 50–70% of the size of fledglings and appeared difficult to kill and consume. Fledglings killed younger conspecifics by striking them with their bills for up to 1 hr or more, and then consumed them by repeatedly striking the carcasses and laboriously tugging small pieces of meat from them.

Older fledglings were particularly skilled at preying on nestlings and appeared to focus their foraging attempts on nestlings to the exclusion of other prey. When a fledgling found an undefended nestling and began to attack it, other fledglings usually came to fight over the victim. In one case, I observed five fledglings attack and consume a 15-day-old nestling that had fallen from its nest.

DISCUSSION

Black-crowned Night-Herons are among the most opportunistic of North American herons. They employ several different foraging behaviors (Kushlan 1976) and consume a wide variety of prey, including fish, mollusks, insects, reptiles, amphibians, rodents, birds, eggs, carrion, refuse, and plants (Hancock and Kushlan 1984, Davis 1993). Night-herons will alter their foraging methods to concentrate on locally abundant resources, including mice (Allen and Mangels 1940), fish (Spanier 1980), and amphibians (Wetmore 1920). They have also been reported to systematically exploit rookeries of other colonially nesting birds, including Common Terns (*Sterna hirundo*; Marshall 1942, Collins 1970, Shealer and Kress 1991) and Franklin's Gulls (*Larus pipixcan*; Wolford and Boag 1971). Kale (1965) reported an instance of adult night-herons in a colony preying opportunistically on White Ibis (*Eudocimus albus*) and Great Egret (*Ardea alba*) chicks from the same mixed-species rookery, noting that ibis and egret chicks from neighboring nests constituted a major food source for night-heron chicks. Published reports of night-herons feeding on conspecifics, however, are limited to Wolford and Boag's (1971) report of a night-heron nestling that was regurgitated by another nestling. Williams and Nicholson (1977) reported a suspected instance of brood reduction in the Black-crowned Night-Heron, but did not find evidence of cannibalism.

There is virtually no information on the foraging behavior of night-heron fledglings during the period immediately after they leave the nest—after the adults have stopped feeding them but before they become adept at catching their own prey. Lorenz (1938) and Palmer (1962) reported that fledglings move through the colony and are able to beg food from any adult; however, Finley (1906) and Noble et al. (1938) found that adults do not feed juveniles on the ground. Data on the composition of fledgling diet are scarce, possibly because recently fledged juveniles may forage at night (Rockwell 1910, Davis 1993). In this study, I found that juveniles sometimes climbed back to the nest in the first 2–3 days after fledging, and were usually fed by the parents. After 3 days post-fledging, fledglings on the ground often grabbed the bills of passing adults in an attempt to stimulate them to regurgitate food, but were almost always unsuccessful.

Fledglings also seemed unable to fish efficiently in the deep water surrounding the island, at least for the first 7 or 8 days after fledging. I frequently observed fledglings in the water striking at floating sticks and pieces of leaves, but they rarely captured live prey. Fledglings occasionally picked up prey dropped by nestlings in active nests; on one occasion, a fledgling climbed into a low nest and pulled a fish from the bill of the fledgling to which it had just been delivered. Adults, by contrast, were never observed feeding on dead nestlings or other carrion, suggesting that they were more skilled at catching higher-quality, live prey.

Although I spent similar amounts of time observing the same rookery each year (1997–2001), cannibalism among Black-crowned Night-Heron fledglings was prevalent only in 2000. I observed night-heron fledglings feeding on dead night-heron and egret chicks only twice in 1998 and once in 2001. The species composition of the nesting colony was fairly constant across years, comprising 120–150 pairs of Black-crowned Night-Herons and 5–10 pairs of Great Egrets and Snowy Egrets; thus, the level of competition for food among fledglings on the island should not have been elevated in 2000. In other years, fledgling diets were dominated by fish and frogs. However, it is difficult to compare prey composition across years because I observed far fewer prey captures in other years, possibly because juvenile Black-crowned Night-Herons may forage mostly at night.

It is possible that cannibalism rates were exceptionally high in 2000 because local shortages of fish or other live prey forced fledglings to seek alternate food resources, but I was unable to document such a shortage. A food shortage would have affected the diet and foraging patterns of fledglings more than adults and nestlings, since adults often left the nesting colony to forage while fledglings remained on the island.

ACKNOWLEDGMENTS

I am grateful to W. E. Davis, Jr., J. A. Kushlan, and an anonymous reviewer for their helpful comments on the manuscript.

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The Wilson Journal of Ornithology 118(1):104–106, 2006

First Report of Black Terns Breeding on a Coastal Barrier Island

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ABSTRACT.—Black Terns (*Chlidonias niger surinamensis*) breed locally in freshwater wetlands across the northern United States and central Canada, often building their nests over shallow water on a floating substrate of matted marsh vegetation. Here, we report the first nesting record of this species on a coastal barrier island. The nest, which consisted of two eggs laid in a slight scrape of sand, was located on 6 July 2004 in a large breeding colony of Common Terns (*Sterna hirundo*) on Kelly's Island at Kouchibouguac National Park, New Brunswick, Canada. The observation also represents the current northeastern breeding limit for this species in North America. Both eggs hatched, but neither chick survived beyond 4 days. *Received 15 December 2004, accepted 5 October 2005.*

The North American subspecies of Black Tern (*Chlidonias niger surinamensis*) breeds locally across the northern United States and central Canada. Black Terns are semicolonial, typically nesting in productive, shallow freshwater marshes, semipermanent ponds, prairie sloughs, and along margins of lakes and rivers (Stewart and Kantrud 1984, Dunn and Agro 1995, Schummer and Eddleman 2003). Nests are generally placed in areas of calm water within stands of emergent bulrush (*Scirpus* spp.), cattail (*Typha* spp.), bur-reed (*Sparganium* spp.), or pickerelweed (*Pontederia cordata*; Cuthbert 1954, Dunn 1979, Mazzocchi et

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al. 1997). Nests are usually built over shallow water (0.5–1.2 m deep) on a floating substrate of matted, dead marsh vegetation, floating rootstalks and discarded pieces of wood, or muskrat feeding platforms; occasionally, nests are built on non-floating substrates, including muskrat lodges, flattened vegetation, and mud (Cuthbert 1954, Bergman et al. 1970, Dunn 1979). Nests often consist of dead vegetation arranged in a compressed pile with a shallow depression at the top (Dunn and Agro 1995).

Black Terns use coastal habitats during migration, winter, and in summer when nonbreeding birds aggregate in large flocks (100+ birds) on saltpans, marshes, estuaries, and brackish wetlands (Dunn and Agro 1995). Reports of Black Terns breeding in marine areas are extremely rare (Sirois and Fournier 1993). In the mid-1990s, a single nest was found at Seal Island National Wildlife Refuge (NWR), Rockland, Maine (C. S. Hall pers. comm.), and in both 2003 and 2004, two nests were located at Machias Seal Island, New Brunswick (C. M. Develin pers. comm.). The nests at these marine sites consisted of a small amount of dead vegetation in sparse common sheep sorrel (*Rumex acetosella*) and grasses, or they were placed on a granite rock surface. Nests were located in large, mixed colonies of Common (*Sterna hirundo*) or Arctic (*S. paradisaea*) terns. The nest at Seal Island NWR was ~30 m from the high-tide line, whereas the nests at Machias Seal Island were ~100 m from water. All five Black Tern nests in marine areas failed to fledge young.

The Canadian Maritime breeding population of Black Terns was estimated to be 150 pairs (Erskine 1992), with southern New Brunswick representing the species' northeastern breeding limit in North America (Dunn and Agro 1995). Since 2000, however, Black Terns (<4 birds annually) have been observed in mid- to late June with breeding Common Terns on four coastal barrier islands of Kouchibouguac National Park, New Brunswick. Surveys conducted from 2000 to 2003, however, did not confirm breeding (Christie et al. 2004; E. Tremblay pers. comm.).

Here, we report the first evidence of Black Terns breeding on a coastal barrier island. Kelly's Island (46° 50′ N, 64° 55′ W), 2 ha in size, is part of a 26-km crescent of barrier spits and islands that separate Kouchibouguac Bay of the Northumberland Strait from the shallow estuary-lagoon system of Kouchibouguac National Park (Beach 1988). The island is composed of sand and is vegetated by extensive stands of marram grass (*Ammophila breviligulata*); the island's outer edge consists of a gently sloping intertidal beach zone. The island supports a large breeding colony of Common Terns, which included 1,041 nests counted in 2004 (Parks Canada Tern Survey 2004).

On 6 July 2004 at approximately 17:00 AST, after the entire tern colony at Kelly's Island had flushed and taken flight, we identified a pair of adult Black Terns flying above the center of the island. One of the Black Terns descended and landed, and we subsequently identified a Black Tern nest with two eggs laid in a slight scrape of sand. The long, oval eggs were noticeably smaller (~34 × 24 mm) than the subelliptical eggs in nearby Common Tern nests (~42 × 31 mm; SRC pers. obs.). The Black Tern eggs were dark olive and marked with dark brown dots and blotches, the density of which was greater near the large end. Nearby Common Tern eggs were generally cream colored and finely marked with brown and black dots. The Black Tern nest and many of the Common Tern nests consisted of a small amount of dead vegetation loosely lining a scrape made in the sand. Both species nested in areas of the island where cover was sparse (5–15% marram grass). Whereas Common Tern nests were 0.5–30 m from the high-tide line, the Black Tern nest was 26.5 m from the water. Two Common Tern nests were within 3 m of the Black Tern nest.

On 20 July at 17:20, we returned to the nest and found a newly hatched chick and a pipping egg. The hatchling's down was predominantly cinnamon and black, except for a white belly and a white mask over the eye and cheek. A single adult Black Tern was observed flying 5–10 m directly above the nest. On 24 July, we checked the nest again and found both chicks dead at the nest; one adult Black Tern was flying 10–15 m above the island. The young were necropsied, but the cause of death was undetermined (S. McBurney pers. comm.).

Adult Common Terns at Kelly's Island readily exhibited aggressive displays toward the smaller Black Tern adults. Overt aggression typically involved brief aerial chases and attack by Common Terns as a Black Tern adult approached and descended toward its nest. Common and Black terns occasionally form mixed-breeding colonies elsewhere (Snow and Perrins 1998), and Common Terns have been known to defend nesting territories against other tern species, including Roseate Terns (*Sterna dougallii*; Burger and Gochfeld 1991, Nisbet 2002). Aggressive displays by Common Terns, and the close proximity of tern nests at Kelly's Island, may have compromised the survival of the Black Tern chicks by preventing the adults from providing sufficient food resources to their young, resulting in dehydration or malnutrition (S. McBurney pers. comm.). Nevertheless, our observations represent the first confirmed breeding of Black Terns on the barrier islands of Kouchibouguac National Park and represent the northeastern breeding limit for this species in North America.

ACKNOWLEDGMENTS

We are grateful to Kouchibouguac National Park, especially E. Tremblay, for providing logistical and field support. We appreciate information on Black Terns provided by the National Audubon Society's Seabird Restoration Program, the University of New Brunswick, and I. C. T. Nisbet. S. McBurney willingly performed necropsies. Observations and preparation of this manuscript were conducted during SRC's graduate studies of Red-breasted Mergansers (*Mergus serrator*) supported by Bishop's University, the Canadian Wildlife Federation, the New Brunswick Wildlife Trust Fund, and the Province of Québec Society for the Protection of Birds. We thank M.-A. Hudson and three anonymous reviewers for helpful comments on this manuscript.

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The Wilson Journal of Ornithology 118(1):107–108, 2006

First Observation of Cavity Nesting by a Female Blue Grosbeak

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ABSTRACT.—On 21 May 2003, we discovered a completed Blue Grosbeak (*Passerina caerulea*) nest in an Eastern Bluebird (*Sialia sialis*) nest box. On 28 May, the nest contained four whitish-tan eggs with light-brown, streaky and spotty markings, an unusual color pattern for Blue Grosbeak eggs. Species' identification was confirmed by capturing the breeding female in the nest box, and confirmed again later with identification of the chicks as Blue Grosbeaks. To our knowledge, this is the first published account of cavity nesting, artificial or otherwise, for this species. *Received 27 September 2004, accepted 31 May 2005.*

The Blue Grosbeak (*Passerina caerulea*) is a large bunting in the family Cardinalidae and is relatively common in the southeastern United States. However, little is known of the breeding ecology of this species (Ingold 1993). The nest is typically cup-shaped and composed of twigs, rootlets, and bark, is often lined with grass and/or fine hair, and sometimes contains artificial debris, such as cardboard, cellophane, or newspaper (Stabler 1959, Bent 1968, Ingold 1993). Blue Grosbeaks commonly build their nests in riparian thickets, fallow fields, open woodlands, and hedgerows, usually from 1 to 4 m above the ground (Stabler 1959, Bent 1968, Ehrlich et al. 1988).

Here, we detail an observation of cavity nesting by a pair of Blue Grosbeaks. We discovered the nest during an ongoing study of Eastern Bluebirds (*Sialia sialis*) in Craighead County, Arkansas. During the winter of 2002, we erected approximately 200 Eastern Bluebird nest boxes at 2 m above ground, with each box being at least 100 m from adjacent boxes. The site is composed mostly of pastures and fallow fields, with some nest boxes located along mixed-hardwood forest edge.

We checked all nest boxes at least once per week to monitor nesting activity. On 21 May 2003, we discovered an unidentified, but complete, nest without eggs in a nest box in an area of open woodland dominated by northern red oak (*Quercus rubra*) and bordered on one side by a thin stand of privet (*Ligustrum* spp.). The nest was an open cup composed of grass, fine sticks, and several interwoven pieces of cellophane. Cellophane is commonly incorporated within nests of Blue Grosbeaks (Ingold 1993), possibly as a substitute for shed snakeskin, a common item in grosbeak nests (Strecker 1926). It is unclear why snakeskins are incorporated into grosbeak nests (Ingold 1993), but their addition to nest boxes with artificial nests may decrease predation (E. C. Medlin and TSR unpubl. data). This behavior is common in some obligate cavity-nesting species, including Tufted Titmouse (*Baeolophus bicolor*) and Great Crested Flycatcher (*Myiarchus crinitus*). We did not measure the nest, but the nesting material entirely covered the floor of the nest box (10 cm wide × 15 cm deep), and the nest cup covered the rear 70% of the nest-box floor. We estimated the inside diameter of the nest cup to be ~6–7 cm, which is similar to grosbeak nest-cup diameters reported by others (Ingold 1993).

On 28 May, we checked the nest again and it contained four oval eggs with light-brown, streaky and spotty markings, and a light, whitish-tan background color. Although Blue Grosbeak eggs are typically light blue to white and unmarked (Ingold 1993), some are lightly spotted with brown (Ingold 1993) or "distinctly marked with dots and spots of chestnut and subdued lilac" (Davie 1898:404). The size, color, and markings of the eggs we observed were similar to those of Brown-headed Cowbirds (*Molothrus ater*), so much so that we could not distinguish them from cowbird eggs. Although Blue Grosbeaks are frequent

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hosts of Brown-headed Cowbirds, and cowbirds are known to parasitize hosts nesting in nest boxes (Whitehead et al. 2000, 2002), we did not observe nest parasitism in any of our nest boxes during our 2-year study.

Prior to the discovery of the nest, we had observed a pair of Blue Grosbeaks near the nest box several times over a 2-week period. We suspected that the pair was nesting nearby, but not in the nest box. On 8 June, however, we captured a female Blue Grosbeak in the nest box by using a nest-box trap (Robinson et al. 2004); she was incubating the four eggs described above, which appeared to be pipping. When we revisited the nest again on 13 June, we found four nestlings approximately 5 days old and apparently in good condition. We identified the nestlings as Blue Grosbeaks (and not cowbirds) by virtue of their large conical bills and yellow rictal flanges. Although Brown-headed Cowbirds also have conical bills, grosbeaks' bills are obviously larger. In addition, Blue Grosbeak chicks have yellow rictal flanges (Baicich and Harrison 1997), whereas those of Brown-headed Cowbird chicks are cream-colored in the eastern subspecies (Baicich and Harrison 1997).

On 27 June, the nestlings were no longer in the nest. We assumed they fledged successfully because there were no obvious signs of nest predation, and predation at our field site is generally low (13% Eastern Bluebird nest predation; TJR and TSR unpubl. data).

Our observation of Blue Grosbeaks nesting in a nest box is unique for two reasons: (1) to our knowledge, this is the first record of cavity nesting by Blue Grosbeaks, and (2) the color pattern of the eggs was unusual. We know of few previously published reports of female Blue Grosbeaks laying eggs with brown spotty markings—a rare color pattern for Blue Grosbeak eggs (Davie 1898, Ingold 1993). Avian ecologists should be aware that cavity nesting occasionally occurs in this species; the behavior may merit closer examination.

ACKNOWLEDGMENTS

We extend our thanks to J. C. Bednarz, H. B. Fokidis, J. L. Ingold, M. A. Whitehead, and an anonymous reviewer for comments on previous versions of this manuscript. Additionally, we appreciate J. Cassady and C. Robertson for their invaluable assistance in the field. This research was funded by an ASU Faculty Improvement Grant to TSR in 2003 and 2004, an Arkansas Audubon Society grant to TJR in 2003 and 2004; TSR further benefited from reassignment time from the Environmental Sciences Program at ASU.

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The Wilson Journal of Ornithology 118(1):109–112, 2006

A New Record of the Endangered White-winged Nightjar (*Eleothreptus candicans*) from Beni, Bolivia

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ABSTRACT.—The ecology of the White-winged Nightjar (*Eleothreptus candicans*) is poorly known. Only three breeding populations (one from Brazil and two from Paraguay) are known, and populations are decreasing due to continuing destruction of *cerrado* habitat. On 14 September 2003, we took several photos of an unidentified nightjar in Beni Biosphere Reserve, Departmento Beni, Bolivia. The bird was later determined to be an adult male White-winged Nightjar. Interestingly, the only previous record for Bolivia was a male collected in 1987 at the same locality and time of year. Because the White-winged Nightjar is nonmigratory and secretive, we hypothesize that there may be a sustainable population of White-winged Nightjars in Bolivia, and the paucity of sightings may be due to the species' low detectability. *Received 16 December 2004, accepted 11 October 2005.*

The White-winged Nightjar (*Eleothreptus candicans*), a member of the Caprimulgidae (Cleere 1999, Pople 2004), was recently reclassified from the genus *Caprimulgus* to the genus *Eleothreptus* (Cleere 2002). Its known range and population size are very small, and its ecology has received attention only recently (Pople 2003). Parker et al. (1996) assigned the species High Conservation Priority and the IUCN lists the species as Endangered (IUCN Red List; Pople 2004). *E. candicans* is threatened by ongoing loss of its *cerrado* habitat (heavy grazing, trampling, invasive grasses, habitat conversion to plantations, and large-scale, uncontrolled grass fires; Cleere 1999, Pople 2004).

Until the 1980s, White-winged Nightjars were known only from two museum specimens collected at the beginning of the 19th century in Oriçanga, São Paulo state, and Cuiabá, Mato Grosso state, Brazil (Sclater 1866). Only three populations have been found, all in southern Brazil and eastern Paraguay: Emas National Park, Brazil (Rodrigues et al. 1999); Aguará Ñu, Mbaracayú Forest Nature Reserve, Paraguay (Lowen et al. 1996, Clay et al. 1998); and a recently discovered population at Laguna Blanca, Departmento San Pedro, central Paraguay (Anonymous 2002). Additionally, in 1987 a single male was captured and collected at the Beni Biological Station, Departmento Beni, Bolivia (Davis and Flores 1994). Despite specific searches for the species in subsequent years, however, it has not been relocated at Beni (Brace et al. 1997, Brace 2000, Pople 2004; R. Brace and J. Hornbuckle *in litt.*).

Surveys in Aguará Ñu have resulted in a population estimate of 40–150 individuals (Clay et al. 1998, Pople 2003) at that location. The number of birds observed in Emas National Park was 12 in September 1985 and only 1 in October 1990 and in November 1997 (Rodrigues et al. 1999). Although there are no other recently published records from Emas, the national park probably supports a sizeable population of *E. candicans* (Pople 2004) because Emas encompasses a large extent of apparently suitable habitat. The recently discovered population at Laguna Blanca in Paraguay is estimated to include a minimum of 30 birds (R. P. Clay *in litt.*).

On 14 September 2003 at 22:00 EDT, we photographed an unidentified nightjar on a termite mound between the Beni Biological Station (Estación Biológica del Beni; 14° 50′ S, 66° 17′ W) and Laguna Normandia (~1.5 km northwest of the station; see Fig. 3 in Brace et al. 1997), Departmento Beni in northern Bolivia. Later the bird was unambiguously identified as a male *E. candicans* (Fig. 1). Because it lacked visible wear on the remiges and pale flecking in the contour plumage, it is probable that the individual had recently completed a molt. If the species undergoes the same pattern of molt in both Beni Biosphere

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FIG. 1. Adult male White-winged Nightjar (*Eleothreptus candicans*) photographed on 14 September 2003 in Beni Biosphere Reserve, Departmento Beni, Bolivia. Photo by R. Šumbera.

Reserve and Paraguay (i.e., replacement of flight feathers in a single post-nuptial molt), it suggests that the species may breed considerably earlier in Bolivia than in Paraguay (where it breeds mainly between September and December).

Beni Biological Station is 180 km west of Trinidad and 50 km east of San Borja on El Porvenir Éstancia. El Porvenir Éstancia lies in the Llanos de Mojos, which is a lowland plain (~200 m elevation) characterized as savanna with forest islands. The habitat where we observed the White-winged Nightjar is a seasonally inundated savanna with a high density of termite mounds (Fig. 2).

Ours is only the second record of White-winged Nightjar in Bolivia, the first having been made in September 1987 (Davis and Flores 1994). Interestingly, both observations were made near Beni Biological Station at the same time of year (11 September 1987 and 14 September 2003). Despite a number of research programs that have been conducted at the station (A. B. Hennessey *in litt.*), there had been no additional records of White-winged Nightjar after 1987. R. C. Brace and J. Hornbuckle (*in litt.*), for example, searched for White-winged Nightjars and conducted mist-netting from mid-July through the end of August every year from 1992 to 1999, but recorded no White-winged Nightjars. Although the White-winged Nightjar is considerably less conspicuous than many other sympatric nightjar species common in Bolivia (R. G. Pople *in litt.*), it seems unlikely that there would be so few observations of the species if the area supported a small resident population. Rather, the two individuals recorded during the last 2 decades may have come from an undiscovered population elsewhere in the northern Bolivian lowlands. However, *E. candicans* is presumed to be a resident species. Indeed, radio-tracking work in Paraguay (Pople 2003) revealed that White-winged Nightjars are year-round residents, and a study of captive birds revealed a post-nuptial molt pattern typical of a nonmigratory species. Therefore, the occurrence of the two individuals at Beni Biological Station during the same time of year may indicate that some birds make local movements, possibly in response to fires (Pople 2004).

FIG. 2. Typical habitat of the White-winged Nightjar—wet savanna with termite mounds providing perches above the surrounding young vegetation. The forest in the background is Florida Fragment south of Laguna Normandia, 1.5 km northwest of Beni Biological Station, Departmento Beni, Bolivia. The photo in Figure 1 was taken within this area. Photo by T. Grim.

Neotropical savannas are under increasing human pressure due to large-scale conversion of grassland habitats to pastures (Marris 2005). Although the White-winged Nightjar is a typical savanna dweller and is adapted to irregular and small-scale fires, it likely has been negatively affected by regular and large-scale burning in recent years (Brace et al. 1997, Pople 2004). Conservation of savanna habitats—including *cerrado*, the primary habitat for *E. candicans*—has been neglected thus far. Because savanna habitats are facing greater threats than Amazonian rainforests, the conservation of *cerrado* habitat should become a top priority in the Neotropics (Marris 2005).

Our observation highlights the importance of Beni Biosphere Reserve for threatened (n = 4) and near-threatened (n = 15) bird species in Bolivia (Brace et al. 1997). Among these 19 species are 11 that rely wholly or partially on savanna habitat. So far, 500 bird species have been reported from Beni Biosphere Reserve (Brace et al. 1997, Brace 2000). We add to this list one more species: on the same day (14 September 2003) that we observed the White-winged Nightjar, we also recorded one Black-throated Saltator (*Saltator atricollis*).

We hypothesize that Departmento Beni in northern Bolivia holds a resident population of *E. candicans*, and that the paucity of records from Bolivia reflects the lack of intensive searches during the correct season and the low detectability of this species. We concur with Brace et al. (1997) that more information on the White-winged Nightjar's status is required, and we hope that our observation provides an impetus for further research on this elusive species.

ACKNOWLEDGMENTS

We are grateful for the detailed and helpful comments and suggestions by R. P. Clay and two anonymous referees. We thank R. C. Brace and A. B. Hennessey for their comments on the manuscript and G. Dryden for reviewing our translation to English.

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The Wilson Journal of Ornithology 118(1):112–113, 2006

Predation of Eared Grebe by Great Blue Heron

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ABSTRACT.—Great Blue Herons (*Ardea herodias*) typically prey upon fish and other aquatic organisms, and they occasionally take small mammals and birds. We observed a Great Blue Heron attack, kill, and attempt to consume an Eared Grebe (*Podiceps nigricollis*). The heron was unable to swallow the grebe, and it abandoned the carcass after approximately 30 min. An examination of the carcass showed that the grebe lacked obvious physical deformities. Our observation, coupled with a similar one nearby, indicates that Great Blue Herons attack and kill birds larger than reported previously. *Received 11 January 2005, accepted 19 September 2005.*

On the morning of 14 November 2004, we witnessed an adult Great Blue Heron (*Ardea herodias*) attack, kill, and attempt to consume an Eared Grebe (*Podiceps nigricollis*) at Oso Flaco Lake (35° 00′ N, 120° 30′ W) in San Luis Obispo County, California. The incident occurred shortly after the heron landed near the grebe and began foraging in shallow (~30 cm deep) water. At approximately 11:25 PST, the heron caught the grebe with a stabbing motion as the grebe swam underwater. The heron then proceeded to subdue the grebe by grasping its neck, shaking it, and submerging it intermittently. After approximately 15 min, the grebe appeared to be dead. At this point, the heron briefly released the grebe to deliver several sharp blows to its head and chest area.

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The heron attempted several times to swallow the grebe, but it had difficulty maneuvering the grebe into its mouth. During one attempt, it was able to maneuver the carcass into position, but the grebe's diameter, its limp wings, or both prevented the heron from swallowing it. After attempting to swallow the grebe for approximately 15 min, the heron abandoned the carcass, preened briefly, and then flew off. The grebe weighed 255 g (weighed after the grebe was frozen and then thawed), and although that is low body weight for this species (Cullen et al. 1999), it is typical of grebes arriving on a wintering area after a migratory flight (Jehl 1997; J. R. Jehl, Jr. pers. comm.). When we examined the grebe, we found no deformities or obvious indications of poor condition (e.g., loss of pectoral muscle).

On the day previous to our observation (13 November 2004), H. R. Pedersen (pers. comm.) observed a Great Blue Heron at Lake Cachuma in Santa Barbara County, California (~130 km southeast of Lake Oso Flaco), capture an Eared Grebe. The heron was foraging and caught the grebe in shallow water, grasped it by the neck in the same manner we witnessed, and submerged it several times. After a brief struggle, the grebe escaped and appeared unharmed (H. R. Pedersen pers. comm.).

We know of no previous reports of Great Blue Herons capturing, killing, and attempting to consume Eared Grebes, or any other bird species of that size; however, McCanch (2003) reported a Grey Heron (*Ardea cinerea*) that had choked to death while attempting to ingest a Little Grebe (*Tachybaptus ruficollis*). Great Blue Herons have a diverse diet that includes songbirds and mammals of various sizes (Peifer 1979, Butler 1992), and they have been observed abandoning large prey items that they were unable to swallow (R. W. Butler pers. comm.). Thus, it is possible that the herons may have targeted the grebes as potential prey items, but were unable to successfully consume them because of their size. Alternative explanations are (1) that the herons mistook the grebes for fish or (2) that the herons were acting to defend a foraging area. Indeed, an observer at Lake Cachuma reported seeing a foraging heron attack and kill an American Coot (*Fulica americana*) with no attempt to eat it (L. R. Mason pers. comm.). The heron we observed, however, expended a substantial amount of effort subduing and attempting to consume the grebe, indicating a deliberate act of predation. Evidently, small grebes are potential prey items for Great Blue Herons, and herons may attack and kill large birds more commonly than is recognized.

ACKNOWLEDGMENTS

We thank K. E. Jirik, the students of the Terrestrial Vertebrate Ecology Laboratory course at the University of California-Santa Barbara, and members of the Pomona Valley and Golden Gate Audubon Societies for their assistance with observations. H. R. Pedersen and L. R. Mason kindly shared their observations of foraging herons; R. W. Butler provided helpful discussion; and J. R. Jehl, N. V. McCanch, and an anonymous reviewer provided valuable comments on the manuscript.

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The Wilson Journal of Ornithology 118(1):114–116, 2006

Abnormal Eggs and Incubation Behavior in Northern Bobwhite

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ABSTRACT.—A long-term (>5 years) study of Northern Bobwhite (*Colinus virginianus*) provided the first record of runt eggs and two observations of prolonged incubation. During 2004, we located two clutches (*n* = 11 and 9 eggs)—laid by the same hen—consisting entirely of runt eggs. Mean length, width, and mass were 18.8 mm, 15.4 mm, and 2.0 g, respectively, 26% of the volume and 24% of the mass of typical bobwhite eggs. Based on our long-term data set for bobwhites (*n* = 3,566 eggs), runt eggs occur at a frequency of 0.56%, within the range (0.02–4.32%) reported for other avian species. The two records of prolonged incubation behavior represented 75 days (326%) and 47 days (204%) beyond the normal incubation period (23 days) of bobwhites. This prolonged incubation behavior is in excess of the time frame reported for most birds exhibiting prolonged incubation (50–100% beyond normal incubation). *Received 31 January 2005, accepted 3 October 2005.*

Documenting anomalies in avian behavior often is an opportunistic endeavor given the rarity of such behavior and the short-term nature (<2 years) of most studies. An ongoing, long-term (>5 years) radiotelemetry project (The South Texas Quail Research Project; STxQRP) on Northern Bobwhite (*Colinus virginianus*) provided us with the opportunity to monitor bobwhite behavior over seven breeding seasons (1998–2004) on the Encino Division of the King Ranch, Inc., Brooks County, Texas. We provide the first record of runt eggs for Northern Bobwhite and two additional records of prolonged incubation behavior.

First record of runt eggs.—Runt eggs, also referred to as dwarf, cock, wind, and witch eggs (Rothstein 1973), are those noticeably smaller than the smallest expected for a given species (Mulvihill 1987; for suggested criteria, see Koenig 1980a). Although runt eggs have been reported for several avian species (e.g., Canada Goose, *Branta canadensis* [Manning and Carter 1977]; woodpeckers [Picidae, Koenig 1980b]; and Eastern Bluebird, *Sialia sialis* [Mulvihill 1987]), they normally occur at low frequencies (~1 per 1,000 to 2,000 eggs; Koenig 1980b, Mallory et al. 2004). Furthermore, runt eggs usually represent only a small proportion of a clutch (Rothstein 1973, Ricklefs 1975, Bartel 1986). Entire clutches consisting solely of runt eggs are extremely rare and have been reported only for Song Thrush (*Turdus philomelos*; M'William 1927), Gray Catbird (*Dumetella carolinensis*; Rothstein 1973), and Eastern Bluebird (Zeleny 1983). We report the first record of runt eggs for Northern Bobwhite and provide estimates of the frequency of such eggs.

On 21 June 2004, we located a radiomarked hen on a nest at the base of brownseed paspalum (*Paspalum plicatulum*). The clutch consisted entirely of runt eggs (*n* = 11). We monitored the hen for several days thereafter, but never located her at the nest site again. We concluded that she had abandoned the nest and we collected the eggs. During the following 5 weeks, the hen again paired with a male, and on 30 July, we documented a second clutch of runt eggs (*n* = 9) in a nest constructed in red lovegrass (*Eragrostis secundiflora*). The hen also abandoned this nest, and we collected the clutch on 2 August.

None of the runt eggs was viable (i.e., none contained yolk). Mean length, width, and mass of the runt eggs (*n* = 20) were 18.8 mm, 15.4 mm, and 2.0 g, respectively. The smallest reported measurements for bobwhite eggs are 26 mm (length) and 22.5 mm (width) (Bent 1932), and 8.2 g (Case and Robel 1974). Koenig (1980a) defined runt eggs as those with a relative volume (length × width^2 × $\pi/6$) <75% of the average. Mean length, width, and mass of bobwhite eggs are 30 mm, 24 mm, and 8.3 g, respectively (Bent 1932, Case and Robel 1974). Thus, the volume and mass

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of the runt eggs we found were only 26% and 24%, respectively, of the average.

We used data from STxQRP and Hernández (1999) to estimate the frequency of runt eggs in Northern Bobwhite. During 1999–2004 of the STxQRP, we located 392 nests and determined clutch size for 297 nests (n = 3,161 eggs). Hernández (1999) located 83 bobwhite nests in Shackelford County, Texas during 1997–1998 and determined clutch size for 35 nests (n = 385 eggs). Based on these combined data (3,546 normal-sized eggs + 20 runt eggs), runt eggs in bobwhites occur at a frequency of 0.56%, which is within the range (0.02–4.32%) reported for other avian species (Koenig 1980b, Mallory et al. 2004).

The mechanisms underlying the production of runt eggs are not entirely understood (Mulvihill 1987). However, runt eggs often are produced after temporary disturbance or damage (e.g., injury or infection) to the reproductive organs (Pearl and Curtis 1916, Romanoff and Romanoff 1949). Instances of entire clutches being composed of runt eggs suggest a congenital defect or permanent injury to the reproductive system (Mulvihill 1987). We presume the bobwhite hen that laid the runt eggs may have suffered from some type of permanent injury to her reproductive organs.

Prolonged incubation behavior.—Prolonged incubation beyond the normal time required for hatching has been reported for many avian species, including Killdeer (*Charadrius vociferus*; Powers 1978), Common Loon (*Gavia immer*; Sutcliffe 1982), and Long-eared Owl (*Asio otus*; Marks 1983). Most birds that exhibit prolonged incubation appear to incubate for at least 50–100% longer than necessary to hatch a clutch (Skutch 1962). Prolonged incubation (56 days) has been reported only once for Northern Bobwhite (Stoddard 1931), which is 33 days (143%) beyond the average incubation period (23 days). We report two additional records of prolonged incubation for Northern Bobwhite.

During our first observation of prolonged incubation, a bobwhite hen exhibited normal incubation behavior during a first nesting, and the eggs successfully hatched on 7 July 2003. However, the hen exhibited prolonged incubation of a second clutch. We discovered the nest on 11 August, and by 8 September, only 1 of 10 eggs had hatched. The female was not observed on the nest between 9 and 25 September, but on 26 September, the hen returned to the nest and resumed incubation until 5 December. Thus, the hen incubated the eggs for 28 days, abandoned the nest for 17 days, and then resumed incubation for another 70 days. The 98 days of incubation was 75 days (326%) beyond the normal incubation period for bobwhites.

We documented the second occurrence of prolonged incubation during the 2004 nesting season. On 18 June, we accidentally flushed an un-radiomarked hen from a nest. We returned to the nest site on 12 July, presuming the clutch had hatched, and found her still incubating the clutch. The hen continued incubating until 27 August, when the clutch was depredated. Assuming the hen had just begun incubation when we first found the nest, she incubated for at least 70 days, or 47 days (204%) beyond the normal incubation period for bobwhites.

Although only 1 of 10 eggs hatched in our first observation of prolonged incubation, Murray and Frye (1957) suggest that the hatching of even one egg is sufficient to satisfy the nesting instinct. In our observation, however, the hen continued incubation even though only one egg hatched. Hurst (1978) observed a similar phenomenon, during which a bobwhite hen continued incubation of partially hatched, dead chicks. The clutch consisted of 10 eggs: 1 infertile, 1 completely hatched, and 8 partially hatched. The eight partially hatched eggs contained fully developed chicks that had pipped and partially ringed their eggshells but had become "entombed." Hurst (1978) did not report the length of time that the hen remained on the partially hatched eggs.

Prolonged incubation is thought to provide a safety margin for eggs that take longer than normal to hatch (Skutch 1962, Holcomb 1970). However, Holcomb (1970) suggested that prolonged incubation would be maladaptive for species capable of renesting. Bobwhites commonly renest two or three times per breeding season, regardless of previous nest fate (Stoddard 1931). Given that the two records of prolonged incubation occurred toward the end (July–August) of the normal nesting season for bobwhites (May–August), the opportunity for renesting was limited and may have contributed to prolonged incubation.

ACKNOWLEDGMENTS

This research was supported by the George and Mary Josephine Hamman Foundation; Amy Shelton McNutt Charitable Trust; William A. and Madeline Welder Smith Foundation; Bob and Vivian Smith Foundation; Robert J. Kleberg, Jr., and Helen C. Kleberg Foundation; Texas State Council of Quail Unlimited; the South Texas, Houston, East Texas, and Alamo Chapters of Quail Unlimited; the South Texas Celebrity Weekend; Quail Associates; private contributions; King Ranch, Inc.; and San Tomas Hunting Camp. We thank B. M. Ballard, D. G. Hewitt, and three anonymous reviewers for providing helpful comments on an earlier version of this manuscript. Data for this research were provided by the South Texas Quail Research Project. This manuscript is Caesar Kleberg Wildlife Research Institute Publication Number 05-112.

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The Wilson Journal of Ornithology 118(1):117–119, 2006

Once Upon a Time in American Ornithology

George Bird Grinnell, the "father of American conservation," was born in 1849. He ultimately would spearhead a movement for the preservation of North American waterfowl, lay the foundation for the national park system, lead the way in ending the commercial taking of wildlife, and help found the American Ornithologists' Union, Boone and Crockett Club, and Audubon Society. Schooled for a time by Lucy Bakewell Audubon, John James Audubon's widow, Grinnell grew up in Audubon Park, the former 12-ha Audubon estate on Manhattan Island in New York City. "Grandma" Audubon's tutelage, hunting experiences with Audubon's grandson, Jack, and frequent visits to the homes of Audubon's sons, Victor and John Woodhouse Audubon—where rifles and shotguns, powder horns and shot, animal trophies, bird paintings, and boxes of bird skins were always about—were formative, and predisposed Grinnell's future as a naturalist and conservationist. At the age of 25, four years after receiving a B.A. from Yale University in 1870, Grinnell was asked by paleontologist O. C. Marsh, head of the Peabody Museum in New Haven, Connecticut, to accompany him on an army-sponsored expedition of the Black Hills, South Dakota. Commanded by Col. George Armstrong Custer, the 60-day expedition set out on 2 July 1874 from Fort Abraham Lincoln, just across the Missouri River from Bismarck, North Dakota. Because trouble was expected from hostile Indians, the military command consisted of 10 companies of the 7th Calvary, 2 companies of Infantry, and a battery of 3 Gatling guns. In all, there were 1,200 men and their horses, wagons, a beef herd, and Indian scouts (Fig. 1). Military goals were to explore unmapped Indian Territory and investigate rumors of gold; the scientists, or "bug hunters" as the military called them, were along to collect specimens and fossils.

The following ornithological event was recorded by Grinnell as he accompanied Custer's exploration of the Black Hills, about 22 months before the battle of Little Bighorn (Greasy Grass). The incident took place in late August as the troops were on their return trip to Fort Abraham Lincoln from the west. Grinnell was subsequently invited to accompany the inglorious 1876 expedition as naturalist, but he had a professional conflict that kept him home. The original reference is Grinnell, G. B. 1875. Zoological Report. Pages 79–102 *in* Report of a reconnaissance of the Black Hills of Dakota made in the summer of 1874. (W. Ludlow). U.S. Army Department of Engineers.—FRITZ L. KNOPF

> August 28.—About 6.30 a.m., while we were halting for a short time on a little knoll, a most interesting and exciting chase came under my observation. The ground was wet from the rain that had but just ceased to fall, and the men were, most of them, standing by their horses, instead of lying asleep on the ground, as is usually the case when a halt is made. I was looking out over the plain, when I observed two birds in rapid flight, approaching the hill where we were standing. They flew with astonishing velocity, and it was but a short time before they were quite near us. From the manner of their flight, I at first thought they were two falcons engaged in play, but a nearer view showed me that the foremost bird was much the smallest, and that it was making most strenuous efforts to escape from its pursuer by darting and twisting from one side to the other, up or down, or by straightforward flight. In one of its turnings it came quite close to the column, and, forgetting in its intense fear its natural shyness, it darted in among the men and horses. The larger bird, a peregrine falcon, as I could now see, hesitated not an instant, but dashed after, following the object of its pursuit in every cut and twist that it made, now passing under the horses, now low over their backs or close to the men's heads. After, perhaps, a minute of rapid pursuit, the smaller bird by a quick double put a group of men and horses between itself and the falcon, and then darted swiftly along the ground to where I was standing, an interested observer. Here, almost exhausted, it

FIG. 1. The 1874 Custer Expedition returning from the Black Hills of South Dakota, photographed by William H. Illingworth. The expedition included 1,200 men and 110 wagons, here seen between the Black Hills and Fort Abraham Lincoln, Dakota Territory, near the modern day South Dakota and North Dakota border. Photograph taken in the vicinity of George Bird Grinnell's account of a Peregrine Falcon (*Falco peregrinus*) pursuing a Passenger Pigeon (*Ectopistes migratorius*). Custer is on horseback in the foreground with his wagon behind him; in the distance, the expedition is aligned in four columns. Grinnell is believed to be one of three individuals (in the middle on a mule) mounted and slightly forward of the expedition. Photo courtesy of the South Dakota State Historical Society–State Archives.

> alighted on the saddle of a horse standing within arm's length of me, and I was able to distinguish that it was a passenger pigeon, (*Ectopistes migratoria*). Meanwhile, the falcon, baffled for a moment, had risen 30 feet in the air, and was hovering over the group, looking for his prey. Hardly ten seconds had elapsed since the pigeon alighted, when he saw his pursuer above him, and, terror-stricken by the sight, the luckless bird darted away again over the open prairie. The falcon followed, and the doubling and twisting recommenced before they had gone a quarter of a mile. The pigeon once tried to regain the shelter of the command, but his relentless pursuer cut him off and drove him toward the plain, and, in a few seconds, by a tremendous burst of speed, caught up to his victim, and, throwing out his powerful feet, seized him, and, without checking his flight, bore him off to

a neighboring butte, there to devour him. It was a splendid sight, and I can compare it to nothing unless it be a scene of ancient falconry, the only difference being that the birds were so much more evenly matched than in the old-time sports. It would, I think, be difficult to name a harder bird to catch than the pigeon, and, perhaps, the only bird that can do it in a straight-away chase is the peregrine falcon. I should mention that the soldiers made efforts to frighten the hawk away by shouting and throwing their hats at it, but it paid no attention to their demonstrations, except once to stretch out its feet as if to grasp a hat that sailed close by it.

The Wilson Journal of Ornithology 118(1):120–127, 2006

Ornithological Literature

Compiled by Mary Gustafson

THE NORTH AMERICAN BANDERS' MANUAL FOR BANDING SHOREBIRDS (CHARADRIIFORMES, SUBORDER CHARADRII). By Cheri L. Gratto-Trevor. North American Banding Council, Point Reyes Station, California. 2004: 45 pp., 4 color plates, 15 figures, 1 table, 8 appendices. Available at no charge from www.nabanding.net/nabanding/pubs.html.—This manual, intended to be an integral part of the North American Banding Council Study Guide, should be required reading for anyone capturing shorebirds (waders). After introductory sections on the ethics of banding and some of the factors to consider when devising a study program, this publication offers a synthesis of the various methods used to capture shorebirds in their breeding, passage, and wintering habitats. This group of species has tested human ingenuity; thus, many of the 180 references from the published literature included in this manual are about trapping techniques. There is also useful material on marking techniques, including bands, color bands, dye-marking, radio tracking, and so on. Although much of this material is available elsewhere, it was scattered in many sources, and it is well worthwhile having it compiled in one publication. The many personal communications add to the book's value, including many of the little tricks that are often passed on by word of mouth.

The manual also includes a useful table that summarizes all that a bander needs to know for each species: American Ornithologists' Union code, Birds of North America reference, band size, methods for determining age and sex, and any problems often encountered when trapping, handling, and banding the species.

As an English ringer of wading birds (albeit with experience in banding shorebirds on four continents), I was struck by the different approach taken in this publication. In many other countries, extensive long-term studies of waders carried out primarily by volunteers have provided ample opportunities to develop methods for safely handling hundreds, and occasionally thousands, of birds at a time. The target audience of this manual, however, is North American banders, who often are professional ornithologists—but inexperienced in studying shorebirds—usually undertaking short-term studies, often of small numbers of birds. Capturing shorebirds can indeed be a specialized art, at times potentially dangerous for birds and for banders, and should not be undertaken lightly. The exceptionally detailed and thorough treatment here, of all aspects of the process, should help ornithologists maximize the scientific value of their work on shorebirds, and minimize the danger to themselves or their subjects. The emphasis throughout is on safe methods of capturing and handling. Given the international knowledge base on these birds—many of which are themselves great international travelers—the author has succeeded in pulling together information from around the world to develop this manual, and all banders can probably learn something from reading it.

There is, unfortunately, one significant failing in the publication—an Appendix on ageing calidrid shorebirds in which the photographs are the worst that I have ever seen published. The birds' feathers are so disheveled that, not only do they reflect poorly on banding, they make it very difficult to discern the plumage characters that the photographs are intended to illustrate. These days, with photographic equipment so easy to use, and, indeed, with so many high-quality images appearing on Web sites and elsewhere, there is no excuse for publishing such poor photographs. The flawed appendix should not detract from the value of this publication, but users of the manual should obtain other reference materials for ageing shorebirds. This useful manual should surely be obligatory reading for all who capture shorebirds.
—DAVID NORMAN, Merseyside Ringing Group, England, and Carnegie Museum of Natural History, Powdermill Avian Research Center, Pennsylvania; e-mail: david.norman@physics.org

A PASSION FOR WILDLIFE: THE HISTORY OF THE CANADIAN WILDLIFE SERVICE. By J. Alexander Burnett. UBC Press, Vancouver, British Columbia. 2003: 331 pp., numerous photos. ISBN: 0774809604, C$85.00 (cloth). ISBN: 0774809612, C$27.95 (paper).—In 1947, in what appears to be an endless series of reorganizations, the Canadian government reorganized the Department of Resources and Government and gave birth to the Dominion Wildlife Service, which carried much of the responsibility for wildlife in Canada. Initially, the agency was staffed by fewer than 30 people, but it included several seasoned ornithologists, including George Boyer and Oliver Hewitt. The early years were challenging—in 1949, Newfoundland and Labrador joined the Canadian Confederation, bringing with them segments of their population that traditionally harvested vast numbers of seabirds and their eggs. In 1950, the Wildlife Service became a division of the National Parks Branch, and chief Harrison secured permission to rename the division the Canadian Wildlife Service (CWS)—the name it still holds today. This book recounts the nearly half-century history of the CWS.

The book is divided into 10 chapters and an epilogue. The first chapter covers the genesis of the CWS and provides an historical context through a synopsis of Canadian wildlife policy up to the 1940s. The remaining chapters are topical, each focusing on an aspect of the CWS's diverse agenda. Chapter 2 describes the CWS involvement in enforcing the Migratory Birds Convention Act of 1917. This included the difficult and sensitive task, conducted by Leslie Tuck and others, of bringing some level of enforcement to the rural populations of Newfoundland and Labrador who depended on seabird harvest for subsistence. Managers required information, and surveys and other scientific research became an integral part of the CWS. Chapter 3 emphasizes working with birds—during the first 50 years of the CWS, ornithology was the preeminent scientific concern. In the early years, waterfowl research tended to dominate the agenda, but seabird research became, and remains, important, and research has been directed at a broad spectrum of problems (e.g., bird strikes at airports). The contributions of prominent CWS seabird biologists (e.g., Leslie Tuck, David Nettleship, Hans Blokpoel, Kees Vermeer, Rob Butler, Tony Gaston, and many others) are chronicled in the chapter.

Chapters 4 and 5 cover mammals and fish, and chapter 6 describes the shift in conservation strategy—from a focus on species to habitat preservation and continental-scale thinking—that began in the 1970s. The chapter also traces changes in the CWS with regionalization of administrative control. Chapter 7 describes efforts to foster public awareness and understanding of wildlife values and, hence, securing public support for conservation initiatives. This involved the cooperation of CWS personnel with filmmakers and the establishment of wildlife interpretation centers. This chapter also tells the painful story of consolidation during the late 1970s and early 1980s, when federal budget cuts caused a thorough reexamination of CWS priorities, as the government cut off funds, for example, for the wildlife interpretation centers.

Chapter 8 deals with the growing field of wildlife toxicology, precipitated by the devastating effects of DDT. It describes programs designed to investigate avian ingestion of crude oil, as well as problems with pesticide use in agriculture and forestry. Chapter 9 covers endangered species, including many birds. Chapter 10, *Defining the Rules: Wildlife Governance,* describes a series of initiatives that had come to fruition by the 1990s (e.g., amendments to the Canadian Wildlife and Migratory Birds Convention acts, Ramsar designation for suitable wetlands sites in Canada, and the Western Hemisphere Shorebird Reserve Network). The Epilogue, *The Canadian Wildlife Service: A Work in Progress,* highlights important aspects of the CWS and brings closure to this historical account.

This book is thoroughly researched and very well written. The author does not shy away from, or gloss over, problems that have been part of the CWS (e.g., federal versus provincial authority, research versus management mandates, or the disastrous budget cuts of the early 1980s). He has managed to provide an even-handed history of the CWS. I am sure that many people who have had careers in the CWS would disagree on details and, perhaps, emphasis, but I find this a well-balanced history of an important North American conser-

vation institution. It should be of interest to any historically oriented ornithologist.
—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

WHALES & DOLPHINS OF THE WORLD. By Mark P. Simmonds, photography by seapics.com. The MIT Press, Cambridge, Massachusetts. 2004: 160 pp., 180 full-color photographs, 1 color map. ISBN 0262195194. $29.95 (cloth).—This book takes on the challenging task of introducing 80-plus species of whales and dolphins to the general public, while at the same time providing many spectacular photographs to get across the author's conservation message. This large-format book (9.5′ × 12.5′) takes advantage of its size by including lots of photos. The photos come from seapics.com, an image library containing the works of over 200 marine and underwater photographers, many of whom are internationally known. This is the marine wildlife equivalent of the bird photo archives provided by VIREO (Visual Resources for Ornithology), and enables the author to illustrate his book with some truly stunning photos, including some of very rare species like that of a breaching Blainville's beaked whale (*Mesoplodon densirostris*). The text is easy to read and clearly written to introduce whales and dolphins to the general public so that people will become more informed about the conservation issues affecting cetaceans. At the same time, the book includes some of the latest scientific findings and taxonomic changes.

The book is divided into 5 chapters. The first 2 chapters cover whale biology, behavior, and some general information for each of the 14 cetacean families. Because some families are poorly known or include fewer species, the general accounts can vary in length from just 2 pages (porpoises and beaked whales) to 12 pages (marine dolphins). The family accounts include both general descriptive information and detailed information, such as breeding biology, habitat, prey, and feeding strategies if known. Each account also includes information on current and past conservation threats, such as whaling and habitat disturbances. There are also short sections on cetacean physiological adaptations, migration, intelligence, and echolocation. The first 2 chapters compose two-thirds of the book (~100 pp.), while the final third (60 pp.) includes a chapter on interactions between man and whales and 2 chapters on conservation threats and current measures being taken to protect cetaceans. At the end of the book is a rather uninteresting 2-page color map of the world showing cetacean habitats; however, it does not include much detail other than basic ocean temperature zones and river dolphin ranges. There is also a nice comprehensive list of all the cetacean species, subdivided by families, that includes Latin names, a bibliography of Web sites and book titles, a very general and basic 1-page glossary, and a page of interesting facts and figures on cetaceans (e.g., the longest-lived mammal—the bowhead whale, *Balaena mysticetus*—can live more than 200 years).

The 180 photographs are what really make this book interesting, especially since it is just 160 pages long. Included are some incredible action shots like an orca (*Orcinus orca*) just about to make a meal of a mako shark (*Isurus oxyrinchus*) and another of copulating Atlantic spotted dolphins (*Stenella frontalis*). My favorite was a photo of a snorkler alongside a sperm whale (*Physeter macrocephalus*) that fills two full pages, although it is somewhat ruined by a large chapter heading on one of the pages. By using photos from seapics.com, the author is able to draw from an almost limitless collection of quality images. Many of the photos appear to be published for the first time in this book, although some have previously appeared in other publications. Nonetheless, the quality of the reproductions is good.

This is an easy book to recommend to anyone with an even slight interest in marine mammals. As stated in the introduction, the book "is intended as both a celebration of the whales and dolphins of the world and an introduction to their diversity, biology and conservation." It certainly meets that goal. The author is the Director of Science at the Whale and Dolphin Conservation Society, and the book is written to promote their conservation views; in fact, the royalties from the book are donated to the society. Whereas several other recent books serve as excellent marine mammal field guides, this book was intended for a wider audience and would make a nice addition to any library. You will probably find yourself looking through and marveling at the photos again and again, as I did.—MICHAEL FRITZ, See Life Paulagics, Seaville, New Jersey; e-mail: mike@paulagics.com

PARTNERS IN FLIGHT: NORTH AMERICAN LANDBIRD CONSERVATION PLAN. By Terrell D. Rich, Carol J. Beardmore, Humberto Berlanga, Peter J. Blancher, Michael S. W. Bradstreet, Greg S. Butcher, Dean W. Demarest, Erica H. Dunn, W. Chuck Hunter, Eduardo E. Iñigo-Elias, Judith A. Kennedy, Arthur M. Martell, Arvind O. Panjabi, David N. Pashley, Kenneth V. Rosenberg, Christopher M. Rustay, J. Steven Wendt, and Tom C. Will. Cornell Lab of Ornithology, Ithaca, New York. 2004: 84 pp. Available at no charge from www.partnersinflight.org.—The long-awaited *Partners in Flight* [PIF] *Landbird Conservation Plan* arrived with much fanfare, and deservedly so. This broad plan will serve as the starting point for bird conservation planning throughout the U.S. and Canada. A future planned revision will incorporate Mexican species, expanding the utility of the plan to the continental scale.

The plan starts with a description of how it was created and how it should be implemented, in addition to definitions of terms and various ranking factors. A total of 448 species that nest in North America are included. Landbirds are defined to include species in 45 families. These families include Cathartidae plus those within the following orders: Galliformes, Falconiformes, Columbiformes, Psittaciformes, Cuculiformes, Strigiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes; 13 more families (including Tinamidae) will be added when the plan is revised to include Mexico. The plan also provides guidance on *Conservation Issues and Recommendations* for seven Avifaunal Biomes: Arctic, Northern Forest, Pacific, Intermountain West, Southwest, Prairie, and Eastern.

At the core of the plan are the PIF Species of Continental Importance, composed of 100 Watch List Species and 91 Stewardship Species. The Watch List Species were determined through Assessment Scores (from 1 to 5) of the Population Size, Breeding Distribution, Non-breeding Distribution, Threats to Breeding Population, Threats to Non-breeding Population, and Population Trend for each individual species. The Combined Score is determined by summing Population Score, the highest of the Distribution and Threats scores, and the Population Trend score, for a maximum of 20.

Species with Combined Scores of 14 and up comprise the Watch List; species with a Combined Score of 13 and a Population Trend of 5 were also added to the Watch List. Six species had Combined Scores of 12 and Trend Scores of 5, including Northern Bobwhite (*Colinus virginianus*), Loggerhead Shrike (*Lanius ludovicianus*), Field Sparrow (*Spizella pusilla*), Lark Sparrow (*Chondestes grammacus*), Black-throated Sparrow (*Amphispiza bilineata*), and Grasshopper Sparrow (*Ammodramus savannarum*). One species, the Eastern Meadowlark (*Sturnella magna*), had a Combined Score of 11 and a Trend Score of 5, but no species had a lower Combined Score and a Trend Score of 5. A whopping 43 species that had Combined Scores of 13 and Trend Scores of less than 5 did not make the Watch List.

Several species rated the maximum score, including Gunnison Sage-Grouse (*Centrocercus minimus*), Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*), California Condor (*Gymnogyps californianus*), Thick-billed (*Rhynchopsitta pachyrhyncha*) and Red-crowned parrots (*Amazona viridigenalis*), Ivory-billed Woodpecker (*Campephilus principalis*), Black-capped Vireo (*Vireo atricapilla*), Florida Scrub-Jay (*Aphelocoma coerulescens*), and Bachman's (*Vermivora bachmanii*) and Kirtland's warblers (*Dendroica kirtlandii*). This varied group includes species absent from the USFWS endangered species list (Gunnison Sage-Grouse, Lesser Prairie Chicken, Thick-billed and Red-crowned parrots), two species that were previously all but written off as extinct but present on the endangered species list (Ivory-billed Woodpecker and Bachman's Warbler), and species that are heavily managed endangered species (California Condor, Black-capped Vireo, Florida Scrub-Jay, and Kirtland's Warbler).

The Population Size Ranking Factor includes a Global Population Estimate, a number difficult to determine for most bird species. I find these estimates to be interesting and thought provoking, though I continue to be puzzled by the disparity in population estimates among species. The percentage of the population residing in the U.S. and Canada is also estimated, and, for many species included in the plan, ≤1% of the global population nests in the U.S. or Canada. Expansion of the plan to Mexico will be critical to future conservation efforts. Although Population Trend information for each species is used as a part of the Combined Score, the information in the Trend Score is qualified by using the Monitoring Needs information. The Monitoring Needs identifies species for which trend data are lacking or imprecise, as well as species affected by poor survey coverage (e.g., those in boreal forests and far northern areas). The remainder of the species that lack an identified Monitoring Need have a qualifier, that while monitoring is considered adequate "some issues, such as bias, may not have been accounted for."

While it is easy to find fault with individual data points or certain aspects of the plan, the utility of the ranking process is evident in the results. Without debating which species are facing threats, what effect those threats might have on a population, or whether a Ranking Factor should be increased or decreased, the plan will be useful for achieving bird conservation at the biome, BCR, state, or habitat level. The plan is a starting point for all future bird conservation efforts. Partners in Flight has recently released revised ranking data for landbirds covered in this plan on the PIF Web site (www.partnersinflight.org). The *Landbird Conservation Plan* should be required reading for biologists and land managers as well as those interested in bird conservation.—MARY GUSTAFSON, Texas Parks and Wildlife Department, Mission, Texas; e-mail: Mary.Gustafson@tpwd.tx.state.us

FLIGHT IDENTIFICATION OF EUROPEAN SEABIRDS. By Anders Blomdahl, Bertil Breife, and Niklas Holmström. Christopher Helm, London, United Kingdom. 2003: 374 pp., over 690 color photos. ISBN: 0713660201. £35.00 (paper).—Field guides to bird identification are no longer restricted to general guides on the birds of a particular region. Although this guide's coverage is restricted to the European region, it covers the specialized topic of flight identification of seabirds, a group defined here as including loons, grebes, tubenoses, cormorants, waterfowl, skuas, jaegers, gulls, terns, alcids, etc. The authors state that they were inspired by their study of large numbers of migrating seabirds along the Baltic coast of Sweden, but much of the information pertains to almost any nontropical coast along the North Atlantic.

The guide opens with a solid *Basics of Field Identification* section. It is a good overview of the challenges inherent to watching fast-flying birds in oftentimes difficult conditions, and contains many cautions for the less experienced birder. The book stresses the shape, size, and flight style of birds in flight. The discussion of weather, wind, and light is helpful for those not used to scanning vast stretches of ocean. Although the next section listing 87 seabird watching sites in Western Europe is not very useful on the U.S. side of the "pond," it is a good guide for traveling North American birders.

Species are organized by functional groups: some by family, such as those in the section entitled "*Divers Gaviidae*"; others more informally, such as those in the section entitled "*Diving Ducks and Sawbills.*" An overview of identification points is provided in each section, including marks that separate species from other groups or from other species within groups, and marks related to age and molt. A blue box on the overview page contains a bulleted list of field marks to note when attempting to separate species within the group. It stands out well for easy reference in the field as that fast-flying seabird goes whizzing past.

The individual species accounts are unique among field guides in that they stress identification in flight. A short opening paragraph describes the species' range and includes other commentary. The accounts contain the more-expected information under the headings *Size* and *Plumage and Bare Parts.* Size information is often presented with a comparison to other species covered by the guide. The accounts also contain the headings *Silhouette* and *Flight and Flocking.* These key features make this guide particularly suited for seabird watching. Again, comparatives are used liberally throughout these sections.

A nice touch is that the authors apparently were not enslaved by format. A *Note, Voice, Subspecies,* and/or *Geographical Variation* section appears at the end of each species account, as warranted. For example, it would not have been very useful to include a description of Fea's Petrel (*Pterodroma feae*) vocalizations, but it is very appropriate that one is included for Canada Goose (*Branta canadensis*). Notes include information such as additional identification points, the possibility of hybrids, the possibility of escapees, and comparisons with other species that, while very rare to the region and not covered in the book, are still possible.

Multiple photographs, all of birds in flight, of course, accompany almost every species account. For those who have become used to the stellar bird photos that have cropped up everywhere these days, some of the photos might seem to be of substandard quality. Many are quite good, but even the more-distant photos do an excellent job of illustrating how the birds actually appear when seabird watching. Photos also include images of birds in various plumages.

This book will be particularly useful as more birders become aware of the massive bird migrations that can be witnessed in many places along the Atlantic coastline. Its emphasis on flight identification complements the more standard field guides available. Use of this guide will speed birders' abilities and confidence as they spend time in the field watching seabirds.

Because this book was written by Europeans for the purpose of identifying European seabirds, North American birders should be aware that some of the book's approaches may be a bit confusing, or less helpful, to them. For example, the common names used in Europe do not always match the names used in North America (e.g., Slavonian Grebe [*Podiceps auritus*] rather than Horned Grebe, Arctic Skua [*Stercorarius parasiticus*] rather than Parasitic Jaeger). In addition, comparisons are often made to European species. For example, "Red-necked Grebe lacks the abnormally elongated appearance of Great Crested Grebe and is a more compact and chubbier bird," but many North American birders are not familiar with Great Crested Grebe (*Podiceps cristatus*). Finally, some species that are fairly regular on the U.S. side of the Atlantic are treated with minor descriptions and no photos (e.g., Canvasback [*Aythya valisineria*] and Redhead [*A. americana*]) or descriptions are missing altogether (e.g., Black Skimmer [*Rhynchops niger*]). Overall, however, this book is worthwhile to those who spend time, or would like to spend time, watching the spectacle of seabird migration along the Atlantic coast.—PAUL A. GURIS, See Life Paulagics, Green Lane, Pennsylvania; e-mail: info@paulagics.com

THE SINGING LIFE OF BIRDS: THE ART AND SCIENCE OF LISTENING TO BIRDSONG. By Donald E. Kroodsma, illustrated by Nancy Haver. Houghton Mifflin Company, Boston, Massachusetts and New York, New York. 2005: 482 pp., 68 figures, CD of recordings. ISBN: 0618405682, $28 (cloth).—"Somewhere, always, the sun is shining, and somewhere, always, the birds are singing." So begins Don Kroodma's celebration of birdsong, *The Singing Life of Birds.* On every page, Kroodsma reveals his passion for birds, his infatuation with birdsong, and his desire to unravel the mysteries of avian singing behavior. More than a celebration, the book is Kroodsma's attempt to answer the "why" questions of birdsong. Why do some species learn their songs? Why are the songs of other species innate? Why do some species have dialects, where birds match the songs of their neighbors? Why would other species be unable to learn neighboring songs? Why do mockingbirds mimic? Why do females of some species sing? Kroodsma attempts to answer such questions with 30 different adventures—30 accounts of birds singing their stories—and shares three decades of recording and analyzing songs. Traveling widely across the Americas—from the eastern to the western U.S. and from Saskatchewan to Central and South America—often enlisting the aid of countess colleagues and students, Kroodsma takes us along on his exploits as he recounts his recording experiences.

The common thread running throughout the book is an emphasis on the *combination* of listening to (songs on the CD) and seeing (sonagrams) bird songs. It is the sight of sound that excites Don Kroodsma, and he infects the reader with his enthusiasm (". . . I can't imagine a world without sonagrams, as I can't imagine listening without also seeing"). Using sound spectrograms and the accompanying CD of bird songs, he considers how birds acquire their songs, what makes their songs unique, what functions songs serve, and "how the pieces of this singing continent fit together."

Chapter 1 introduces readers to the elements of sonagrams—how to interpret the time-frequency displays of sonagrams; how to distinguish noisy, complex sounds from pure-toned, whistled sounds; how to recognize the rhythm and amplitude evident in sonagrams; and how to learn to listen ("How do I hear with my eyes?"). Kroodsma also shares his personal beginnings and interest in birdsong in this chapter, crediting the Bewick's Wren (*Thryomanes bewickii*) as the bird that first taught him how to listen. He ends the chapter by outlining the kinds of questions he asks, and attempts to answer, throughout the book: How, where, when, and from whom do birds acquire their singing vocabulary? What are the functions of different bird sounds? How do a bird's life history features and its evolutionary background influence song? How do the brain, syrinx, and hormones control and influence birdsong?

As Kroodsma takes readers on his pre-dawn vigils, he reflects on the music of nature and the journeys on which birds have taken him. He bikes across Martha's Vineyard, astonished to hear and record improbable *sweetie-heys* from Black-capped Chickadees (*Poecile atricapillus*) (across the continent, nearly all other chickadees sing *hey-sweetie*). He traipses across, canoes through, flies to, and crisscrosses, visits, and revisits Illinois, South Dakota, New York, North Carolina, Michigan, California, Colorado, Saskatchewan, Iowa, and Nebraska—all to identify "The Great Marsh Wren Divide" that distinguishes what are almost certainly two different species of Marsh Wren (*Cistothorus palustris*). Kroodsma spends an entire early-May night (20:10–05:04), following one male Whip-poor-will (*Caprimulgus vociferus*), and counts 20,898 *tuck-*WHIP*-poor-WILL*s—2,300 songs/hr and 40 songs/min in just under 9 hr. And then he asks "Why so much song?" (Because the moon was full? Because the weather was warm? Because Whip-poor-wills had just returned from migration? Do high song rates reflect genetic superiority or good territories?). Relentlessly curious, always intrigued, Kroodsma is continually searching for answers.

Kroodsma's enthusiasm is one of the most notable and enjoyable features of his book. I offer only a few examples: (1) "Hear the DNA of this flycatcher speak. . . "; (2) "I love the way song 'G' begins. . . "; (3) "There's something universal in the quality of these sounds [of Sooty Shearwaters, *Puffinus griseus*], and it seems fitting that the birds themselves have the final comment about the sheer wonder and joy of birdsong"; (4) ". . . I can't help but. . . admir[e] how the black images of songs against the white paper reveal the magic in the singing bird"; and (5) ". . . songs of some [Fox Sparrows, *Passerella iliaca*, are] so beautiful that they can bring tears to the eyes."

Kroodsma shares many of his discoveries about birdsong with readers. For example, there are two birdsong vocabularies and two species (eastern and western) of Marsh Wrens, not just one. The songs of Eastern Phoebes (*Sayornis phoebe*) and Willow (*Empidonax traillii*) and Alder (*E. alnorum*) flycatchers are innate, not learned. Sedge Wrens (*Cistothorus platensis*) improvise (make up their songs) and they do not imitate (learn songs from) their neighbors as other wrens do—because Sedge Wrens are nomadic due to the unpredictability of their sedge-meadow breeding habitats. Song Sparrows (*Melospiza melodia*) that match and share songs with their neighbors keep their territories longer—and may live longer. A young Bewick's Wren learns his father's songs early in life, but in the following years, after occupying a territory of his own, he replaces his father's songs by matching those of neighboring males. Kroodsma also lets us in on the fact that the *meetcha* song "switch" of a male Chestnut-sided Warbler (*Dendroica pensylvanica*) is "off" if he has a female, but it is "on" if he is without a female (males sing several *meetcha* songs, e.g., *wheedle wheedle wheedle wheedle sweet sweet MEETCHA*).

There are 68 figures, nearly all of which are sonagrams; these are flawless and impeccably prepared and presented. Some sonagrams are presented at an expanded time scale to show greater detail, and songs of these sonagrams can also be heard on the CD, but are played at a correspondingly slower pace. Figure captions offer straightforward explanations about how to interpret the notes and "read" the sonagrams; Kroodsma points out the intricate details and encourages readers to follow along on the CD—to hear, and see, birdsong at the same time. The CD (98 tracks, ~73 min) contains superlative recordings of more than 50 species—to aid readers in the interpretation of the sonagrams or for sheer listening enjoyment.

Appendix I (*Bird Sounds on the Compact Disc*) provides detailed, colorful descriptions of the bird sounds on the accompanying CD. Appendix II (*Techniques*) offers useful advice on how to listen to and record birdsong, on the recording equipment needed to do so, and on the software for making sonagrams. At the end of Appendix II, Kroodsma notes that "There's no longer any mystique to what I have done all these years. Anyone can do this kind of stuff. And anyone should." The *Notes and Bibliography* chapter provides a short section on recommended readings, an annotated list of readings for the key topics discussed in text, and a formal, extensive bibliography. A well-organized, all-inclusive index—referencing key topics, CD tracks, the locations of sonagrams in text, and the most important information for the key species discussed—completes the volume.

Cautious, meticulous, thoroughly prepared, objective, and determined to know, Kroodsma takes the reader, with lively, often stirring prose, on 30 fascinating journeys. No matter what your level of ornithological expertise, after reading this book you will have learned to listen to, and to look at, birdsong in a different way, and you will have broadened your understanding of avian singing behavior. As Kroodsma reminds us (quoting Shakespeare), "The earth has music for those who listen." I highly recommend this book.—JAMES A. SEDGWICK, USGS Fort Collins Science Center, Fort Collins, Colorado; e-mail: jim_sedgwick@usgs.gov

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The Wilson Journal of Ornithology

Volume 118, Number 2, June 2006

Published by the
Wilson Ornithological Society

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THE WILSON JOURNAL OF ORNITHOLOGY
(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th St., Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Blvd., Ste. 680, Waco, TX 76710.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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

FRONTISPIECE. Bachman's Sparrows (*Aimophila aestivalis*) occupy fire-dependent, longleaf pine (*Pinus palustris*) ecosystems of the southeastern United States. Tucker et al. (p. 131) found that both densities and reproductive indices were greater during the first 3 years after burning than in older burns; they recommend a 2–3 year burn regime to maintain healthy populations. Similarly, Stober and Krementz (p. 138) report that home-range size increases with habitat succession: home ranges in mature habitats often were twice the size of those in regeneration habitats. Original painting (watercolor) by Don Radovich.

The Wilson Journal
of Ornithology

Published by the Wilson Ornithological Society

VOL. 118, NO. 2 June 2006 PAGES 131–280

The Wilson Journal of Ornithology 118(2):131–137, 2006

BREEDING PRODUCTIVITY OF BACHMAN'S SPARROWS IN FIRE-MANAGED LONGLEAF PINE FORESTS

JAMES W. TUCKER, JR.,[1,3,5] W. DOUGLAS ROBINSON,[1,4] AND JAMES B. GRAND[2]

ABSTRACT.—Bachman's Sparrows (*Aimophila aestivalis*) occupy fire-dependent, longleaf pine (*Pinus palustris*) ecosystems of the southeastern United States. Their populations have declined, due, in part, to fire suppression and degradation of longleaf pine forests. Populations decline when longleaf stands go more than 3 years without fire. The influence of fire on breeding productivity, however, is poorly understood because territories are large and it is difficult to find the well-hidden nests of this ground-nesting sparrow. In an earlier study, densities of Bachman's Sparrows were similar across pine stands burned 1 to 3 years previously, but declined significantly by the 4th year since burning. To assess whether the decline in density might be associated with a decline in breeding success, in 2001 we used a reproductive index to estimate breeding productivity of 70 territorial males, and from 1999 to 2001 we monitored 28 nests. We examined the influence of (1) season (growing versus dormant) when last burned and (2) years since burning on breeding productivity of Bachman's Sparrows in longleaf pine stands in the Conecuh National Forest, Alabama. Reproductive indices were greater ($Z = 1.99$, $P = 0.047$) during the first 3 years after burning (mean = 3.8, SE = 0.4, $n = 10$) than they were 4 years after burning (mean = 2.0, SE = 0.5, $n = 3$), similar to the pattern of change in Bachman's Sparrow density. We found no effect of burn season on the breeding productivity index ($Z = 0.075$, $P = 0.94$). The parallel patterns of declining density and lower breeding success suggest that Bachman's Sparrow density may be positively correlated with habitat quality. We conclude that burning longleaf pine forests on a 2–3 year rotation will best maintain populations of Bachman's Sparrows. *Received 8 February 2005, accepted 25 November 2005.*

Bachman's Sparrow (*Aimophila aestivalis*) is one of the bird species most characteristic of longleaf pine (*Pinus palustris*) forests and it ranks high among species of management concern in the southeastern United States (Hunter et al. 1994). It is classified as threatened or endangered in several states (Dunning 1993) and in 2002 it was red-listed (i.e., one of most at-risk species) by the National Audubon Society on its WatchList (see http://audubon2.org/webapp/watchlist/viewSpecies.jsp?id=18). Loss and degradation of habitat are the most probable causes for the species' population decline (Haggerty 1988). Prescribed fire has been identified as a key tool for managing Bachman's Sparrow habitat (Plentovich et al. 1998,

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Tucker et al. 1998). Until recently, however, prescribed fire has been used mainly during the winter (dormant season) to minimize its negative effects on sparrow reproductive success, despite evidence that historically, natural fires occurred most often during late spring and summer (growing season; Robbins and Myers 1992). Growing-season fires are most beneficial to native plant communities (e.g., Platt et al. 1988, Waldrop et al. 1992, Streng et al. 1993), but the way in which fire timing influences sparrow breeding success is unknown.

Similarly, evidence from botanical studies indicates that frequent fires are needed to maintain dense, herbaceous ground cover preferred by Bachman's Sparrows (e.g., Platt et al. 1988, Dunning and Watts 1990, Waldrop et al. 1992, Streng et al. 1993, Plentovich et al. 1998, Tucker et al. 1998). Engstrom et al. (1984) followed changes in bird species composition through 15 years of fire exclusion in a stand of "oldfield pines" (mostly loblolly, *P. taeda*; and shortleaf, *P. echinata*, pines) in northwestern Florida that had previously been burned annually during the dormant season; Bachman's Sparrows disappeared from the stand after 5 years of fire exclusion. In studies on Florida dry prairies, Bachman's Sparrow densities increased on sites burned in mid-June relative to those on control sites (≥2.5 years since burning; Shriver et al. 1999), but there were no differences in density or reproductive success during the first three breeding seasons following winter fires (Shriver and Vickery 2001). Yet, no data are available to evaluate directly the influence of time since burning and season of burning on breeding productivity of this elusive sparrow species.

In a previous study, we examined the influence of burn season and fire frequency on the density of Bachman's Sparrows in longleaf pine forests in southern Alabama and northwestern Florida (Tucker et al. 2004) and found that density was unaffected by burn season. Furthermore, density was similar within the first 3 years after burning, but declined precipitously in stands 4 or more years after a fire (Tucker et al. 2004). We hypothesized that reduced breeding success in stands unburned for 4 or more years might explain this decline in density. To test this hypothesis, we compared the breeding productivity of Bachman's Sparrows across burned units of longleaf pine habitat that differed in time since burning. We also evaluated the potential influence of fire timing within the growing season on nesting success by comparing daily survival rates between nests initiated early and late in the growing season.

METHODS

We estimated breeding success by monitoring nests and using a reproductive index based on behavioral observations (Vickery et al. 1992b). The reproductive ecology of Bachman's Sparrows is poorly known because nests are hidden on the ground, usually below tufts of overhanging grasses, and are therefore exceptionally challenging to locate (Weston 1968, Harrison 1975, Haggerty 1986). In response to the difficulties of finding ground-nesting sparrow nests, Vickery et al. (1992b) developed a reproductive index based on readily observable behaviors that reduces the necessity of locating nests to measure breeding success (Vickery et al. 1992a, Dale et al. 1997). During the breeding season of 2001, we monitored the territories of 70 male Bachman's Sparrows in longleaf pine stands of the Conecuh National Forest, Alabama. To complement this intensive study of focal individuals, we monitored nests found in the same habitat units from 1999 through 2001.

Between 22 April and 12 May 2001, we located territories within 13 habitat compartments (a group of adjacent stands managed as a prescribed burn unit), which varied from 387 to 700 ha in size and comprised four treatment combinations of burn season (dormant [1 October–31 March] or growing [1 April–30 September]) and time since burning (1–3 years or 4 years). We sampled two compartments for each treatment but one: there was only one compartment that had been burned during the growing season 4 years earlier (i.e., 1997). No stands were burned during the 2000 growing season, so territories within stands the 1st year after growing-season burning could not be included. Because the number of compartments was small and the study design was unbalanced, we grouped compartments burned ≤3 years earlier to test our hypotheses that reproductive success would parallel trends in density (Tucker et al. 2004) and be greater during the first 3 years (n = 10) than 4 years (n = 3) post-burning.

Female and juvenile Bachman's Sparrows are very secretive and difficult to observe, so we concentrated our efforts on searching individual territories, rather than mapping territories within habitat compartments, to increase our chances of observing evidence of reproduction. Furthermore, Bachman's Sparrow territories are relatively large (see Dunning 1993) and densities are relatively low, especially in stands not burned for ≥4 years (Tucker et al. 2004); thus, monitoring individual territories also allowed us to sample a sufficient number of territories to characterize breeding productivity within each burn treatment (i.e., each combination of burn season and years since burning). Within each compartment, we selected territories for monitoring by visiting an area known to contain several Bachman's Sparrows and selecting the first four or six singing males encountered within each compartment. Although unmated males of many species sing more frequently than mated males (Best 1981), the territories that we monitored within habitat compartments were adjacent to each other (although often separated by ≥100 m) and we did not observe evidence (e.g., appearance of additional territories) that would suggest that we overlooked mated birds during selection of the territories. We monitored 10 territories within each burn treatment, but we divided territories unequally between the two habitat compartments within treatments to allow a team of two observers traveling together to efficiently monitor two habitat compartments (i.e., 5 territories per observer) each day. We marked singing perches for each male with plastic flagging and noted the territorial boundaries and location of adjacent territories not selected for study. We also used mist nets to capture most of the males (53 of 70) and marked them with unique combinations of colored leg bands. All 70 territories were monitored once per week from 21 May to 12 July 2001, spanning the peak of breeding activity at our study site.

Behavioral evidence of reproductive activity was monitored during 45-min visits to each territory once per week. A visit began when we arrived on a territory, and entailed recording all evidence of reproductive activity—the primary objective being the discovery of an active nest. In addition, we marked new song perches to delineate more accurately territory boundaries. Each territory was assigned a cumulative score indicating increasing evidence of breeding success, slightly modified from the method of Vickery et al. (1992b). The scores for evidence of reproductive success were assigned as follows: 1 = presence of the territorial male, 2 = presence of a mated pair, 3 = evidence of an active nest, 4 = adults carrying food to presumed nestlings, 5 = direct observation or evidence of fledglings, 6 = evidence of an active nest after successful fledging of a first brood, 7 = evidence of successful fledging for two broods, 8 = evidence of an active nest after successful fledging of two broods, and 9 = evidence of successful fledgling for three broods. Bachman's Sparrows are not known to attempt more than three broods within one breeding season (Stober and Krementz 2000).

A cumulative reproductive score corresponding to the maximum evidence of breeding success was assigned to each of the 70 territories. Because individual territories within habitat compartments were not independent sampling units, we calculated median reproductive scores for each compartment and treated individual compartments as our sampling units. The reproductive scores were ranked (i.e., ordinal) data, so we used a nonparametric normal approximation to the Mann-Whitney *U*-test (Zar 1984) to compare median reproductive scores in compartments burned ≤3 versus 4 years previously and compartments burned in the growing versus dormant season.

All Bachman's Sparrow nests found from 1999 through 2001 were monitored according to standard methods (Martin and Geupel 1993) on a 2–3 day schedule until the nests failed or the offspring fledged. We calculated daily survival rates (DSR) of nests (Mayfield 1961, 1975) to evaluate the influence of burn season, years since burning (≤3 versus 4), and timing of fire within the growing season on nesting success. For Mayfield calculations, we used our observations for length of the incubation period (13 days) and nestling period (9 days), which were similar to those reported by Haggerty (1986, 1988). Overall nest success (i.e., the probability of a completed clutch producing ≥1 fledgling) was calculated by raising daily nest survival to the 22nd power. We calculated variances in DSR and evaluated effects by examining 95%

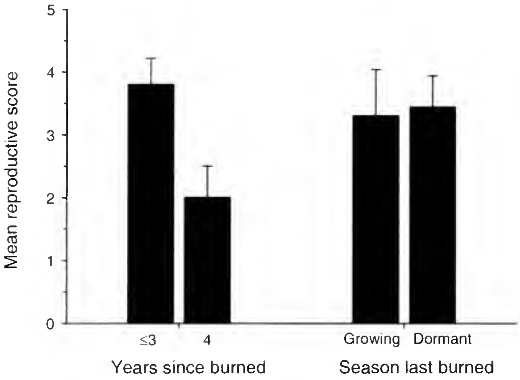

FIG. 1. Mean (± SE) reproductive scores of Bachman's Sparrows calculated using median scores from individual habitat compartments at the Conecuh National Forest, Alabama, during 2001 were greater in the first 3 years after burning (n = 10) than 4 years after burning (n = 3) but did not differ between seasons when last burned (n = 5 and n = 8 for growing and dormant seasons, respectively). Reproductive scores were collected using methods modified from Vickery et al. (1992b).

confidence intervals (±2 SE) around the DSR (Johnson 1979).

RESULTS

Breeding productivity.—Of the 70 Bachman's Sparrow territories monitored, we found evidence of successful reproduction (i.e., fledglings observed) within 30 and evidence of two successful broods within 4 territories. Overall, 28% (14/50) of territorial males in compartments burned ≤3 years earlier remained unpaired, and 50% (10/20) of territorial males in compartments burned 4 years earlier remained unpaired ($\chi^2 = 3.07$, $P = 0.080$). Furthermore, 52% (26/50) of territories in compartments burned ≤3 years earlier successfully produced young, but only 20% (4/20) of territories burned 4 years earlier successfully produced young ($\chi^2 = 5.97$, $P = 0.015$). Reproductive scores of Bachman's Sparrows were greater ($Z = 1.99$, $P = 0.047$) in the first 3 years after burning (mean = 3.8, SE = 0.4, n = 10) than 4 years after burning (mean = 2.0, SE = 0.5, n = 3) but did not differ ($Z = 0.075$, $P = 0.94$) between stands burned in the growing season (mean = 3.3, SE = 0.7, n = 5) versus those burned in the dormant season (mean = 3.4, SE = 0.5, n = 8; Fig. 1).

Nesting success.—We found 34 nests during the study: 2, 12, and 20 in 1999, 2000, and 2001, respectively. Two nests were found the day of fledging, two were destroyed during construction, and two were burned during egg laying, leaving 28 nests for calculating DSR. Overall, 13 of the 28 (46%) nests fledged young. All nest failures resulted from depredation; no parasitism by Brown-headed Cowbirds (*Molothrus ater*) was observed.

DSR of early-season nests (found in April and May) were slightly greater than those of late-season nests (found June and July), although the 95% confidence intervals overlapped (Table 1). In addition, DSR of nests dur-

TABLE 1. Exposure days (number of nests), number of nest failures, daily survival rates (DSR), and 95% confidence intervals (95% CI) by nesting stage and time within the breeding season (nest cycle) for 28 Bachman's Sparrow nests in the Conecuh National Forest, Alabama, from 1999 through 2001.

					95% CI[a]	
Stage	Nest cycle[b]	Exposure days	Failures	DSR	Lower	Upper
Incubation[c]	Early	66.0 (8)	2	0.970	0.928	1.012
	Late	52.5 (8)	1	0.981	0.943	1.019
	Total	118.5 (16)	3	0.975	0.946	1.004
Nestling[d]	Early	64.5 (13)	5	0.923	0.856	0.989
	Late	46.5 (12)	7	0.850	0.745	0.954
	Total	111.0 (25)	12	0.892	0.833	0.951
Combined[e]	Early	130.5 (15)	7	0.946	0.907	0.986
	Late	99.0 (13)	8	0.919	0.864	0.974
	Total	229.5 (28)	15	0.935	0.902	0.967

[a] Calculated as mean ± 2 SE (Johnson 1979).

[b] Early nest cycle included nests found in April and May; late nest cycle included nests found in June and July.

[c] Incubation stage included a 13-day period from laying of the penultimate egg until the first egg hatched.

[d] Nestling stage included a 9-day period from 1st day of hatching until fledging.

[e] Includes the sum of incubation and nestling periods.

ing the incubation period tended to be greater than during the nestling period, but again the 95% confidence intervals overlapped (Table 1). DSR of all nests from the beginning of incubation through fledging was 0.935 (Table 1), and the probability of a completed clutch producing at least one fledgling was 0.226. DSR was similar between the first 3 years (DSR = 0.94, 95% CI = 0.90–0.97, *n* = 22 nests) and the 4th year (DSR = 0.93, 95% CI = 0.86–1.00, *n* = 6 nests) after burning and between sites burned in the growing (DSR = 0.89, 95% CI = 0.81–0.97, *n* = 7 nests) and dormant (DSR = 0.95, 95% CI = 0.92–0.99, *n* = 21 nests) seasons.

DISCUSSION

Nesting success averaged across all our habitat compartments was 23%, which falls within the range previously reported for Bachman's Sparrows in Arkansas pine forests (25%; Haggerty 1988), South Carolina clear-cuts (8–34%; Stober and Krementz 2000), and Florida dry prairies (7–38%; Perkins 1999). Neither burn season nor time since burning had a large effect on nest survival rates at our study sites. Although our sample size of nests was one of the largest yet obtained in a Bachman's Sparrow study, the sample was nevertheless relatively small, indicating that only large effects could be detected (Johnson 1979). In contrast, our results from the reproductive scores (i.e., 70 territories; Fig. 1) suggested that breeding productivity was greater the first 3 years after burning than in older burns. The latter result is consistent with our hypothesis that reduced breeding success in older burns may help explain the lower densities of Bachman's Sparrows in those burns (Tucker et al. 2004).

Although logistic constraints prevented us from simultaneously measuring density and breeding productivity of Bachman's Sparrows, our results suggest a positive correlation between the two measures in our study area. We acknowledge that these results only are suggestive of a positive association between density and breeding productivity, but our consistent results among the 3 years of our studies—1999 and 2000 for density of Bachman's Sparrows (Tucker et al. 2004) and 2001 for this study of breeding productivity—strongly support the conclusion that a regime of burning every 2–3 years will best maintain healthy populations of Bachman's Sparrows in longleaf pine forests. Bock and Jones (2004) reviewed studies that examined the association between avian density and reproductive success and found that a preponderance of studies in relatively undisturbed areas reported a positive association between the two measures; most studies that reported a decoupling between the two measures were conducted in disturbed habitats. Our study area was within the largest remaining extent of longleaf pine forest (Outcalt and Sheffield 1996), and habitats were relatively natural and managed under a paradigm of ecosystem management. Thus, a positive correlation between density and breeding productivity of Bachman's Sparrows in the area would be expected.

Why do density and breeding success decline in older burns? Previous studies suggest that percent coverage by herbaceous ground cover, particularly grass (Dunning and Watts 1990, Plentovich et al. 1998, Haggerty 2000, Tucker et al. 2004), is a primary factor influencing habitat occupancy by Bachman's Sparrows. Herbaceous ground cover and, thus, habitat suitability decreases with time since burning (Engstrom et al. 1984, Tucker 2002). Haggerty (1998) found that territory sizes were inversely correlated with percent coverage of herbaceous ground cover. Thus, higher sparrow densities are facilitated by smaller territories in high-quality habitat.

It should be noted that small territory sizes could have an effect on detectability of reproductive status, as well. The stealthy behavior of female and juvenile Bachman's Sparrows makes them difficult to detect, but they may be easier to detect in smaller territories (i.e., higher quality habitat) because their activities are confined to a smaller area. Despite a potential bias in detectability resulting from territory size, the scores for reproductive success nevertheless would be positively correlated with habitat quality.

Future studies should address the effects of timing of fires within the breeding season. We were unable to examine breeding productivity immediately before and after growing-season fires. Although we did not find differences in sparrow reproductive success between burn seasons, timing of fire *within* the growing season may be an important factor and needs additional study. For example, both our study

(Table 1) and one in South Carolina (Stober and Krementz 2000) revealed that early-season nests tended to be more successful than late-season nests. Fires during late April and early May could destroy a large percentage of the nestlings or young fledglings from the first nesting cycle and result in low annual recruitment from those nesting attempts. Furthermore, we do not yet know whether territory holders move to unburned sites and breed elsewhere or quit all reproduction efforts for a given year when their territories are burned early in the growing season (Seaman and Krementz 2000). Alternatively, productivity of food resources (i.e., seed production and invertebrates) may be enhanced sufficiently by early-season fires to compensate for the loss of nests early in the season; if vegetation re-grows quickly enough, it could provide cover for nests that season. Although Seaman and Krementz (2000) found that Bachman's Sparrows abandoned stands burned in the growing season and failed to return within 50 days after the fires, anecdotal observations (JWT unpubl. data, J. B. Dunning pers. comm.) suggest that Bachman's Sparrows often return and/or establish territories in burned stands within a few days after fire and remain there through the remaining breeding season. Shriver et al. (1996, 1999) found that burning Florida dry prairies during mid-June resulted in an extended breeding season for Florida Grasshopper Sparrows (*Ammodramus savannarum floridanus*) but fires in July did not.

In conclusion, results of this study on breeding productivity and our earlier study on density of Bachman's Sparrows (Tucker et al. 2004) suggest that land managers interested in providing habitat for Bachman's Sparrows in longleaf pine forests should burn at least every 3 years, regardless of burn season. Sites left unburned for ≥4 years host few to no breeding Bachman's Sparrows (Tucker et al. 2004) and it appears that breeding productivity is low among birds that do settle in those habitats. Thus, low breeding productivity may be a plausible explanation for the low densities of sparrows in pine stands unburned for more than 3 years. Because most natural fires historically occurred during the growing season (Robbins and Myers 1992), prescribed burning during the growing season probably will be most beneficial for longleaf pine communities overall. Our study, based on one of the largest sample sizes of reproductive success yet obtained for this elusive sparrow, suggest that burn season may be of little consequence to the reproductive output of Bachman's Sparrows; however, the effects of fire timing within the growing season still need to be evaluated.

ACKNOWLEDGMENTS

This research was supported by funds from the U.S. Geological Survey, State Partnership Program; a J. L. Landers Research Award of the Gopher Tortoise Council; grants from the U.S. Geological Survey, Biological Resource Division, Species at Risk Program; a F. M. Peacock Scholarship from the Garden Club of America administered through the Cornell Laboratory of Ornithology; and the W. F. Coxe Research Fund of the Birmingham Audubon Society. The research benefited from partnerships among the following organizations and agencies: Department of Biological Sciences, Auburn University; Solon Dixon Forestry Education Center, School of Forestry and Wildlife Sciences, Auburn University; Alabama Cooperative Fish and Wildlife Research Unit; USDA Forest Service, Conecuh National Forest; Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries; and The Longleaf Alliance. R. Johnson, G. Morgan, R. Lint, P. Brinn, and R. Mullins provided logistical support during fieldwork. Help from the following field assistants is gratefully acknowledged: C. Krissman, C. Romagosa, J. Stratford, R. Peters, A. Sorenson, and M. Hershdorfer. Reviews by J. B. Dunning, Jr., C. A. Haas, L. A. Powell, P. C. Stouffer, P. D. Vickery, and an anonymous reviewer greatly improved this manuscript.

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The Wilson Journal of Ornithology 118(2):138–144, 2006

VARIATION IN BACHMAN'S SPARROW HOME-RANGE SIZE AT THE SAVANNAH RIVER SITE, SOUTH CAROLINA

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ABSTRACT.—Using radiotelemetry, we studied variation in home-range size of the Bachman's Sparrow (*Aimophila aestivalis*) at the Savannah River Site (SRS), South Carolina, during the 1995 breeding season. At SRS, sparrows occurred primarily in two habitats: mature pine habitats managed for Red-cockaded Woodpecker (*Picoides borealis*) and pine plantations 1 to 6 years of age. The mean 95% minimum convex polygon home-range size for males and females combined (n = 14) was 2.95 ha ± 0.57 SE, across all habitats. Mean home-range size for males in mature pine stands (4.79 ha ± 0.27, n = 4) was significantly larger than that in 4-year-old (3.00 ha ± 0.31, n = 3) and 2-year-old stands (1.46 ha ± 0.31, n = 3). Home-range sizes of paired males and females (n = 4 pairs) were similar within habitat type; mean distances between consecutive locations differed by habitat type and sex. We hypothesize that a gradient in food resources drives home-range dynamics. *Received 16 December 2004, accepted 28 November 2005.*

The Bachman's Sparrow (*Aimophila aestivalis*) is a species of concern due to its population decline (Sauer et al. 2004) and large reductions in range (Dunning 1993). The impact of prescribed fire and timber management on Bachman's Sparrow abundance (Dunning and Watts 1990; Gobris 1992; Plentovich et al. 1998; Tucker et al. 1998, 2004) and habitat occupancy (Wan A. Kadir 1987; Haggerty 1998, 2000) have been well documented. The sparrow's secretive nature, however, makes it difficult to obtain basic information on its reproduction, survival, movement, and home-range dynamics (Dunning 1993).

Bachman's Sparrow home-range sizes have been estimated using spot mapping of unmarked (McKitrick 1979, Meanley 1990) and color banded (Haggerty 1998) males, but this approach is problematic in some habitats because detecting Bachman's Sparrows is difficult in dense, early successional stands (Bibby et al. 1992). Bachman's Sparrows are extremely cryptic in dense vegetation, particularly after 3–4 years of vegetative succession in rapidly growing pine plantations. Males are often only seen while perched on singing posts; such observations do not accurately reflect their entire home range. Because females do not sing, it is impossible to consistently follow or locate their movements. Using spot mapping, mean estimates of home-range size ranged from 5.1 ha ± 1.2 SD (range = 4–6.7, n = 6) in mature Florida pine flatwoods (McKitrick 1979) to 2.5 ha ± 0.2 SE (range = 0.7–4.5, n = 25) in several Arkansas clearcuts during the initial 3 years of succession (Haggerty 1998). How home-range sizes vary across the species' range or habitat types is unknown (Dunning 1993). Because of widespread conservation concern for Bachman's Sparrows, wildlife managers require a better understanding of the species' natural history. We estimated home-range size using radiotelemetry in early and late successional longleaf pine (*Pinus palustris*) stands, examined how home-range size varied with habitat type, and monitored movements within territories by habitat type and sex.

METHODS

During the 1995 breeding season, we studied Bachman's Sparrows at the Savannah River Site (SRS) (33° 14′ N, 81° 31′ W), an 800-km^2 National Environmental Research Park managed by the U.S. Department of Energy. The SRS is located in western South Carolina along the Savannah River in Aiken, Barnwell, and Allendale counties and lies in the Upper Coastal Plain physiographic province. At the SRS, Bachman's Sparrows inhabit understory grass and grasslands found in mature loblolly

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(*Pinus taeda*) and longleaf pine stands (40–98 years old) managed for Red-cockaded Woodpeckers (*Picoides borealis*); they also occur in regenerating pine stands during the initial 6–10 years after planting (Dunning and Watts 1990, Gaines et al. 1995, Kilgo and Bryan 2005). Mature pine stands were managed with periodic prescribed fires on a 3- to 5-year rotation during both the growing and dormant seasons. All mature stands in which we monitored sparrows had been burned 1–2 years previously and were on a 3-year burn rotation. Both the mature and regenerating stands were characterized by understories dominated by *Andropogon* spp. and *Panicum* spp. grasses, rather than native wiregrass (*Aristida* spp.; Stober 1996). Regeneration stands consisted of areas recently clear-cut and machine planted with bare-root longleaf pines at densities of 1,400–1,700 trees/ha; site preparation generally included a prescribed burn before planting. Patches of shrubs within understories of grasses and forbs occurred in both regeneration and mature stands. We randomly selected five stands from groups with similar management histories: one 2-year-old stand (19.2 ha), one 4-year-old stand (15.0 ha), and three mature stands (17.6, 16.7, and 5.2 ha). Selected stands were >1 km apart.

To capture Bachman's Sparrows, in each stand we placed 25 12-m-long (30-mm mesh) mist nets in a 5 × 5 grid with nets 50 m apart (Krementz and Christie 1999). Captured birds were weighed, sexed, aged, and banded with a federal leg band. We categorized sparrows as either hatch-year or after-hatch-year and determined sex by the presence or absence of a brood patch (Pyle et al. 1987). Using the Rappole and Tipton (1991) thigh-harness method, we attached radio transmitters to 20 sparrows in five stands: 6 sparrows (4M:2F) in 2-year-old longleaf pine habitat, 6 sparrows (4M:2F) in 4-year-old longleaf habitat, and 8 sparrows (6M:2F) in three mature pine habitats. The radio with harness weighed 1.1–1.2 g (Advanced Telemetry Systems, Isanti, Minnesota), about 6% of body mass relative to all captured birds (females: 18.6 g ± 0.24 SE, $n = 36$; males: 18.2 g ± 0.31 SE, $n = 69$; Stober 1996, Krementz and Christie 1999). Within a few hours after release, all radio-tagged sparrows resumed normal activities, and we observed no unusual behaviors associated with the radio-attachment method.

We located radio-marked sparrows daily, and made observations on each sparrow throughout the day, from sunrise to twilight, throughout the breeding season. We recorded status (live, dead, or lost radio), location, and any reproductive, foraging, or other behavior. Occasionally, we monitored individuals twice a day, with a minimum of 2 hr between observations. Sparrows readily traversed their home ranges within this time period; therefore, consecutive observations likely did not result in autocorrelation problems (Swihart and Slade 1985) that would have yielded underestimates of home-range size (Cresswell and Smith 1992).

To provide an index of Bachman's Sparrow density, we also conducted spot mapping three times in each stand by using playback tapes of the Bachman's Sparrow's primary song and counting all males (Bibby et al. 1992, Dunning et al. 1995, Stober 1996). While recording daily locations of marked sparrows, we also mapped the locations of unmarked sparrows within each stand. Counter-singing exchanges between unmarked and marked individuals were recorded as well.

We marked sparrow locations with flagging, and we used a Trimble Pathfinder Pro GPS (3-D mode) unit to establish benchmark Universal Transverse Mercator (UTM) coordinates within each territory. All GPS locations were differentially corrected and were accurate to <5 m. Individual locations were then referenced to an established UTM location using a survey laser. The survey laser was used to calculate distance (±0.10 m) and azimuth (±0.01 degrees) between locations, which were then converted into UTM coordinates. Once an individual's locations were mapped, we used program HOME RANGE (Ackerman et al. 1990) to estimate the 95% minimum convex polygon (MCP) for home range (Mohr 1947). We attempted to collect 35 observations per bird (Ackerman et al. 1990). We recognize that the 95% MCP has certain limitations, but all other breeding season home-range sizes for Bachman's Sparrows described in the literature were estimated using this metric (Dunning 1993). Distances moved between locations were calculated for each individual, as were distances from each location to the arith-

TABLE 1. Home-range size estimates and densities of male Bachman's Sparrows in pine habitats, by stand age, during the 1995 breeding season at the Savannah River Site, South Carolina.

Stand age (years)	Stand size (ha)	No. marked sparrows	95% MCP[a] (SE)	Range	Male density/ 10 ha[b]
2	19.2	3	1.46 (0.31)	0.99–2.04	2.59
4	15.0	3	3.00 (0.31)	2.80–3.37	4.65
Mature	17.6	3	—	—	3.41
Mature	16.7	1	—	—	1.79
Mature (both stands)[c]		4	4.79 (0.27)	4.23–5.69	

[a] Mean 95% minimum convex polygon estimates.

[b] Includes both radio-marked and unmarked singing males; densities determined using spot mapping technique within each stand.

[c] Home-range estimate for mature stands is pooled across the two stands.

metic center of each home range, defined as the mean distance from the estimated central coordinate to each observation within the home range.

Only 14 of the 20 radio-marked sparrows were included in the analysis of home-range size. We obtained <35 locations for two females and one male, and three males were treated as outliers and excluded from analyses. The outliers included (1) a bird with two distinct home ranges (a combined total of 20.9 ha) in a mature stand, (2) one whose home range (1.63 ha) ended up outside the study stand in an adjacent 33-year-old stand of planted pine, and (3) one (in the 2-year-old habitat) that behaved like a floater and used part of an adjacent 43-year-old stand of pine (5.46 ha). Due to these exclusions, we used only two (the 17.6- and 16.7-ha stands) of the three mature pine stands in our analyses.

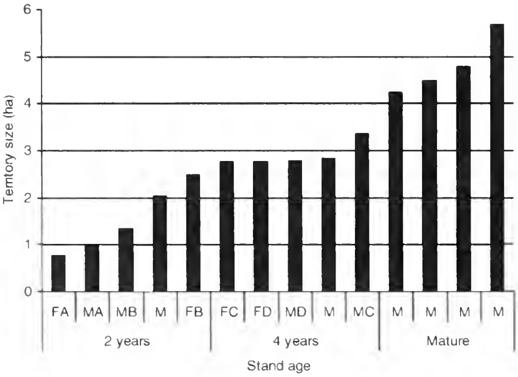

FIG. 1. Home-range size, by habitat age (2 years, 4 years, mature), using 95% minimum convex polygon estimates for Bachman's Sparrows (n = 4 females, 10 males) during the 1995 breeding season, Savannah River Site, South Carolina. Pairs designated by similar alpha characters (A–D); F = female, M = male.

We used a general linear model procedure (PROC GLM; SAS Institute, Inc. 1987) to conduct three pre-planned tests comparing home-range sizes of males by habitat type. We included only males because all marked females were paired to marked males. Once we determined differences in home-range sizes by habitat type (F-test), we used Tukey tests to compare the least-squares means. Due to insufficient sample sizes, we did not test for the effect of sex (female $n = 4$) or conspecific density ($n = 4$) on home-range size. We also used the GLM procedure and Tukey tests to compare the least-squares means for mean distance moved and distance from home-range arithmetic center by habitat type and sex. All statistical tests were one-tailed. The level of statistical significance was set at 0.05 and means are reported ± SE.

RESULTS

For the 14 radio-marked individuals in our analyses, we recorded an average of 63 locations (range = 45–81) per individual over an average of 50 days of observation (range = 38–62 days). Ten birds were monitored in the 2-year-old (3M:2F) and the 4-year-old (3M:2F) stands, and four males were monitored in the two mature stands (3M:0F and 1M:0F). The mean 95% minimum convex polygon home-range size for males and females combined ($n = 14$) across all habitats was 2.95 ha ± 0.57. Mean 95% MCP home-range size across all habitats was 3.26 ha ± 0.49 for males ($n = 10$; Table 1) and 2.20 ha ± 0.48 ($n = 4$) for females. For males, home-range size increased with habitat age ($F_{2,7} = 33.9$, $P < 0.001$; Fig. 1). Home-range sizes differed between 2-year-old (mean = 1.46 ha ± 0.31, $n = 3$) and 4-year-old (mean = 3.00 ha ±

0.31, $n = 3$) regeneration habitat ($t = 3.54$, $P = 0.009$), and were significantly larger in mature pine habitats than in the 2- and 4-year-old habitats ($t = 8.18$, $P < 0.001$; $t = 4.40$, $P = 0.003$, respectively).

Home ranges were always adjacent to a stand edge. Conspecific density was highest (4.65 males/10 ha) in the 4-year-old stand (Table 1) and lower in the 2-year-old stand and one mature stand, both of which were isolated with no suitable adjacent sparrow habitat. Of the four sparrow pairs in which both the male and female were marked, two inhabited the 2-year-old stand and two inhabited the 4-year-old stand. In one pair, the female had a larger home-range size than the male (pair B; Fig. 1); otherwise, male and female home ranges were roughly similar.

Mean distance moved between consecutive observations was 83.9 m ± 12.78 ($n = 14$); distance moved differed among habitat types ($F_{2,11} = 14.66$, $P < 0.001$) and was marginally different between sexes ($F_{1,12} = 3.73$, $P = 0.077$). Mean distance moved in mature stands (106.6 m ± 6.4) was not different from that in the 4-year-old stand (88.8 m ± 5.7), but differed from the distance moved in the 2-year-old stand (61.0 m ± 5.7). The mean distance from the arithmetic center of an individual's home range to each location differed by habitat type ($F_{2,11} = 12.69$, $P = 0.001$), but not by sex ($F_{1,12} = 0.78$, $P = 0.40$). Mean distance from arithmetic center in mature stands (81.8 m ± 4.7) was not different from that in the 4-year old stand (73.6 m ± 4.2, $t = 1.32$, $P = 0.21$) but differed from that in the 2-year-old stand (51.9 m ± 4.2, $t = 4.77$, $P < 0.001$). The longest movement between daily observations was 824 m by a male, and most long-distance movements were about 200 m. In one case, a male crossed a riparian area 200 m wide to an adjacent regeneration stand, remained there for 2 days, and then returned to the original stand.

DISCUSSION

Because we located birds through radiotelemetry rather than by visual documentation at singing posts, our estimates of home-range size were slightly larger and more precise than those reported by Haggerty (1998). Home-range estimates of McKitrick (1979) and Haggerty (1998) were biased by their dependence on visual records of males (color banded or unmarked) perched in conspicuous locations. Nonetheless, home-range sizes of male sparrows in our study were similar to those reported by Haggerty (1998), with the smallest territories found in the 1- and 2-year-old pine regeneration habitat and home range increasing with succession of habitat. Radiotelemetry also allowed us to obtain the first estimates of female home-range size, which were similar to male home-range size ($n = 4$ pairs). Home-range size between paired birds is probably influenced by the mate-guarding behavior that males exhibit during the breeding season (Haggerty 1986). Some locations for the female whose home range was larger than the male's (2-year-old stand) were recorded after her brood had fledged, which may explain the larger size of her home range.

We recorded few instances of direct conflict between adjacent sparrows defending home ranges. The persistent use of primary song and counter-singing (Meanley 1990, Dunning 1993) apparently mediated the need for direct conflict in establishing and maintaining home ranges. Spot mapping revealed the highest density of sparrows in the 4-year-old stand. Similarly, spot mapping conducted by Stober (1996) in regeneration habitats 1–6 years of age revealed that Bachman's Sparrow densities were greatest in 3- to 4-year-old habitats. Overlap of sparrow home ranges was limited to three instances and occurred in grassy patches in mature pine stands or in regeneration habitats where trees and shrubs were suppressed and grasses dominated the vegetation.

Although Haggerty (1986) reported that sparrow density was inversely related to home-range size, we were unable to corroborate this. Stober (1996) found more sparrows in stands with suitable adjacent habitat than in isolated, disjunct stands. Dunning et al. (1995) also found that areas connected by corridors of suitable habitat had a greater probability of sparrow occupancy than isolated patches of suitable habitat. Greater conspecific density may constrict the size of home ranges in breeding season, but this hypothesis needs to be tested by removing territorial individuals and monitoring the behavior of adjacent individuals. Vegetation succession and arthropod food resources also may play important roles in determining home-range size.

We found that home-range size increased with habitat succession: home ranges in mature habitats often were twice the size of those in regeneration habitats. We hypothesize that the distribution of resources within home ranges may explain this pattern. Bachman's Sparrows are omnivorous, foraging exclusively from the ground for insects (orthopterans, arachnids, lepidopteran larvae, coleopterans, hemipterans) and grass seeds, especially those of *Panicum* spp. (Allaire and Fisher 1975, Haggerty 1992, Dunning 1993). Early successional habitats have greater arthropod productivity than mature pine stands in the Southeast (Menhinick 1963, Landers and Mueller 1986, Hurst 1992). Cross (1956) surveyed a range of upland habitats at the SRS for Orthoptera and found >40 species in early successional habitats compared with only 7 species in mature loblolly pine stands. In contrast, ground-level arthropod communities in mature pine stands managed for Red-cockaded Woodpeckers at the SRS include an abundance of spiders and ants, but few grasshoppers (New and Hanula 1998). Stober (1996) found that, as a percentage of total vegetation cover, *Panicum* spp. were more abundant in regeneration stands (0.8–1.3%) than in mature pine stands (0.1–0.4%); thus, differences in home-range size between habitats may be a reflection of greater seed resources and arthropod productivity in early regeneration habitats than in mature pine habitats managed for Red-cockaded Woodpeckers. In examining previous studies on Bachman's sparrows across their range (Wan A. Kadir 1987; Dunning and Watts 1990; Gobris 1992; Haggerty 1998, 2000; Plentovich et al. 1998; Tucker et al. 1998, 2004), we observed that, in general, sparrow densities and arthropod communities were reduced with succession of understory vegetation.

Despite the differences we observed in home-range sizes by habitat type and the differences in male densities among stand ages, Stober and Krementz (2000) detected no significant differences in survival rates between sexes or habitat types. Apparently, the larger home-range sizes of Bachman's Sparrows in mature pine stands do not predispose those birds to lower survival rates, as might be expected from longer movements throughout their territories. Breeding season survival rates were high (0.905, 95% CI = 0.794–0.992), with only 2 mortalities (raptor and mammal depredations) out of 20 individuals radio-tagged.

We found that Bachman's Sparrows did not move far (~100 m/day) between consecutive observations, as was also found for radio-marked Eastern Towhees (*Pipilo erythrophthalmus*) at the Savannah River Site (Krementz and Powell 2000). Like towhees, Bachman's Sparrows moved among adjacent stands, but unlike towhees, Bachman's Sparrows used middle-aged (~20- to 35-year-old) stands infrequently (Stober 1996). Not surprisingly, we found that daily movements reflected home-range sizes: smaller home ranges among habitat types were associated with shorter daily distances moved.

Management for Bachman's Sparrow populations in forested habitats often involves prescribed fire and reduced pine densities. If small home-range size is a surrogate for habitat suitability, managers should maintain a continuous matrix of herbaceous understory vegetation. Clear-cuts should be managed for perches (Dunning and Watts 1990), abundant herbaceous vegetation (Mills et al. 1991, Dunning 1993), and connectivity with nearby suitable habitat (Dunning et al. 1995). Although it is known that mature stands of pine become more suitable for sparrows with frequent prescribed fire and moderate basal areas of pine, further research should ascertain whether home-range size in mature pine stands is dependent on the distribution of herbaceous understory, as arthropod communities in mature pine stands are a function of primary productivity occurring on the forest floor (Cross 1956). Additional information on Bachman's Sparrow reproduction and survival across the range of occupied habitats is needed to determine the viability of populations inhabiting intensively managed industrial forests versus forests managed on longer logging rotations with fire management.

ACKNOWLEDGMENTS

This project was funded by the USGS Biological Resources Division and by the U.S. Department of Energy—Savannah River Operations Office through the U.S. Forest Service—Savannah River under Interagency Agreement DE-AI09-00SR22188 (Cooperative Agreement contract no. 12-11-008-876). J. C. Kilgo, G. O. Ware, J. B. Dunning, Jr., J. Blake, and two anonymous reviewers commented on the manuscript. Thanks to J. S. Christie, A. Allen, H. McPherson, C. E. Moorman, and J. B. Dunning, Jr., for assistance in the field.

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The Wilson Journal of Ornithology 118(2):145–151, 2006

NESTING SUCCESS AND BREEDING BIOLOGY OF CERULEAN WARBLERS IN MICHIGAN

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ABSTRACT.—The Cerulean Warbler (*Dendroica cerulea*) is a Nearctic-Neotropical migratory bird species that has declined significantly over the long-term. Poor reproductive success may be an important factor contributing to the observed decline, but reproductive output has been measured for very few breeding populations. From 2003 to 2005, I intensively monitored 22–23 breeding territories/year in each of two large forest habitats in southwestern Michigan: oak- (*Quercus* spp.) hickory (*Carya* spp.) (2003: Barry State Game Area) and black locust- (*Robinia pseudoacacia*) black cherry (*Prunus serotina*) (2004–2005: Fort Custer U.S. Army Michigan National Guard Reservation). I also gathered descriptive data on nonsong vocalizations and age of territorial males. I describe four distinctive call notes, by sex, including the social and environmental contexts in which they were used. Using two independent methods of aging, there was a strong preponderance of after-second-year males at both study sites. Only 9 (n = 7 nests), 12 (n = 14), and 30 (n = 25) fledglings were produced during the 2003, 2004, and 2005 breeding seasons, respectively. Nest heights were the highest recorded for this species (mean = 19–20 m). During the same period, male reproductive success was 0.30, 0.32, and 0.80 male fledglings/breeding male and 0.60, 0.63, and 1.58 fledglings/breeding pair. Productivity estimates, not thought to be self-sustaining, were even lower than those of a well-studied Cerulean Warbler population in southern Ontario. Thus, reproductive output was low in two geographic regions—representing three different forest types—in the northern portions of the Cerulean Warbler's breeding range. The preponderance of after-second-year males at the Michigan study sites and in southern Ontario suggests a need for regional models of Cerulean Warbler population dynamics. *Received 21 March 2005, accepted 22 December 2005.*

The population declines and conservation status of Nearctic-Neotropical migratory bird species are the subjects of much debate (Askins 1993, Martin and Finch 1995, Robinson et al. 1995, James et al. 1996, Faaborg 2002). The Cerulean Warbler (*Dendroica cerulea*) is a Nearctic-Neotropical migratory bird species that has declined significantly over the long-term throughout its breeding range, prompting a recent petition to the U.S. Fish and Wildlife Service to assign the species threatened status under the Endangered Species Act (U.S. Fish and Wildlife Service 2002). Breeding Bird Survey data (1966–2000) indicate a population decline of 3.04%/year (Link and Sauer 2002). In Canada, the Cerulean Warbler is a Species of Special Concern (Committee on the Status of Endangered Wildlife in Canada 2003).

Populations of Cerulean Warblers may be negatively affected by numerous alterations to their breeding habitats, including the loss of large tracts of mature deciduous forest, forest fragmentation and associated negative factors (e.g., increased brood parasitism and nest predation), increasing forest immaturity via accelerated harvest cycles, and loss of key tree species (Robbins et al. 1992, Hamel 2000). Despite a recent increase in studies of breeding Cerulean Warblers (Oliarnyk and Robertson 1996; Jones et al. 2000, 2001, 2004; Gabbe et al. 2002), critical information concerning nest success and breeding biology in different parts of the breeding range remains scarce. Because the Cerulean Warbler is apparently expanding its range along a northeastern front (Hamel 2004), northern populations may be important to its continued persistence. My objectives were to (1) gather data on nesting success in two distinct forest habitats (oak-hickory, locust-cherry) in southwestern Michigan, and (2) describe the age structure of breeding populations and the social context of nonsong vocalizations, both poorly known for this parulid species. Because certain vocalizations may be given near the nest by breeding adults, the study of nonsong vocalizations is important in evaluating nest productivity (Barg 2002).

METHODS

Study sites and periods.—I studied nest success and breeding biology in two large forest tracts in southwestern Michigan known to har-

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bor breeding populations of the Cerulean Warbler (Barrows 1912, Brewer et al. 1991, Rosenberg et al. 2000). Site 1 is a 1,813-ha tract of largely unfragmented oak- (*Quercus* spp.) hickory (*Carya* spp.) and black walnut (*Juglans nigra*) forest in the Barry State Game Area (BSGA), Barry County, Michigan (42° 35′ N, 85° 26′ W). BSGA is currently managed for multiple wildlife conservation purposes, including the production of game and nongame species. The site was originally abandoned farmland purchased piecemeal by the state of Michigan in the 1940s; because of natural succession, the forest at BGSA is now relatively mature. The topography is low rolling hills and depressions. Site 2 is a 2,849-ha black locust (*Robinia pseudoacacia*) and black cherry (*Prunus serotina*) forest in the Fort Custer U.S. Army Michigan National Guard Reservation (FTCU), Kalamazoo County, Michigan (42° 18′ N, 85° 19′ W). The site was obtained as farmland and scattered homesteads by the U.S. government in 1917. The topography is gentle hills with little relief. BSGA and FTCU are 35 km apart, separated by a landscape of small towns, small woodlots, marshes, lakes, and farmland. Both sites are characterized by maturing forest with large trees, occasional gaps, and an open understory—all habitat features preferred by Cerulean Warblers. I studied Cerulean Warblers at BSGA from 2 June to 27 July 2003, and at FTCU from 15 May to 23 July 2004, and from 19 May to 25 July 2005.

Territory mapping, nest monitoring, and nest-site characteristics.—In 2003 and 2004, I mapped Cerulean Warbler territories according to Bibby et al. (2000), whereby foci of territorial male activity are the primary means of identifying individual breeding territories. At each site, males were often recognized by song type (several frequently gave a distinctly less-buzzy ending to their typical song), plumage variation (several had a distinct white supercilium), and differences in their stage of the reproductive cycle. I marked locations of male song perches on USGS 1:24,000 topographic maps that were enlarged (by computer) 3×; enlarged maps showed topographic detail clearly, including specific recognizable ridges, depressions, small wetlands, and roads. Mapping revealed preferred (tall) trees from which individual males repeatedly sang throughout the breeding season, usually in the center of the territory. I gained additional information on territory boundaries by following males as they patrolled and sang throughout their territories, and by observing boundary disputes (counter-singing and direct fights involving male-male contact). I color-banded 14 territorial males in 2005 at FTCU, 10 of which subsequently aided me in determining territory boundaries that year; the remainder were on territories that I did not monitor. All males captured and banded were used in an analysis of age structure. Established territory boundaries were evident by mid-June at both sites. Global Positioning System coordinates were determined for estimated territory centers and plotted on topographical maps.

I intensively searched territories every 2–6 days (0.5–2.0 hr/visit) for the presence of active nests or newly fledged young; I observed territories from 06:00 to 16:00 EST, with occasional evening visits from 16:00 to 21:30. Each territory check involved a complete traverse through the entire territory, with stops in and near all forest gaps to search for active nests and adults giving contact calls. I monitored nests every 2–4 days early in the nesting cycle, and every day as fledging neared. I defined successful nests as those from which ≥1 warbler young fledged; failed nests were those from which no warblers or only Brown-headed Cowbirds (*Molothrus ater*) fledged. Most nests were very high (19–20 m) in the canopy and nest contents could not be observed directly. I used a spotting scope (20–60×) to observe female incubation and brooding behavior, and to count warbler and cowbird nestlings as they grew large enough to be seen above the nest rim. As fledging approached, large cowbird young were easily distinguished from the much smaller warbler young by plumage features, size, and vocalizations. Fledglings recently fledged from previously undiscovered nests ($n = 9$) were counted directly when they emitted loud begging calls. To minimize underestimating Cerulean Warbler reproduction, I identified to species and recorded the locations of all begging fledglings and alarm-calling adults of all avian species in all foliage layers of each Cerulean Warbler territory.

After each nest had failed or the young had fledged, I recorded the following nest-tree and nest characteristics: nest-tree species; nest height (distance from ground to nest bottom); nest-tree height (distance from ground at stem base to highest foliage); trunk distance (distance from nest to central tree axis, measured from the ground); foliage distance (distance from nest to nearest foliage below it); nest-tree diameter at breast height (dbh); and gap distance (distance from nest to any obvious forest discontinuity ≥25 m^2). Height ratio was calculated as nest height/nest-tree height. All heights were measured with a rangefinder except foliage distance, which was estimated by eye (nearest meter). I measured trunk distance and gap distance with a transit.

Estimating age of territorial males.—Age of breeding male Cerulean Warblers was estimated using two methods. Method 1 (2004–2005), which provides a general estimate of male age-class frequency, entailed using 10 × 32 binoculars to observe whether the bird had a distinct white supercilium, purportedly present only in second-year (SY) males and absent in after-second-year (ASY) males (Dunn and Garrett 1997); nearly all males were observed from ≤15 m. Method 2 (2005) was conducted by an experienced bird bander, who relied on a combination of molt limits and the colors of flight and body contour-feathers (Pyle 1997) to age the 14 captured territorial males while they were in hand. The two investigators using the two different aging methods recorded ages independently of one another.

Nonsong vocalizations.—When monitoring nests and territories for reproductive output, I described nonsong vocalizations emitted by both sexes of Cerulean Warblers and documented the social and environmental context of those vocalizations. The resulting set of descriptions likely represents the most common nonsong vocalizations that this species makes on the breeding grounds. I did not make audio recordings and sonograms of these vocalizations; rather, I described them with previously established terminology used for describing vocalizations of wood warblers (Nolan 1978, Getty 1993).

RESULTS

Territory defense.—From mid- to late May each year, I often observed male Cerulean Warblers at FTCU engaged in territorial chasing and occasional physical fights ($n = 5$ observed). Observations of the BSGA population began in early June, when males had already established territories and were no longer chasing one another. Throughout June and much of July at both sites (and in mid- to late May at FTCU), males sang prodigiously, often within 10–30 m of one another during bouts of intense counter-singing at their territorial borders; counter-singing sometimes involved three males.

Nonsong vocalizations.—Adult Cerulean Warblers emitted four distinct nonsong vocalizations over the 3-year study. (1) Both sexes gave a metallic, buzzy *zzee* call note, singly or in series of 1–6 notes. I heard female *zzee* calls 127 times, and knew the behavioral context of 87: 23 occurred when females were foraging alone or with the male or a fledgling nearby; 33 when near, leaving, or approaching an active nest; 29 when at an active nest; and 2 (a series of loud *zzees*) occurred when my presence near the female's nest apparently caused alarm. Males gave only 24 *zzee* calls, with the behavioral context known in 23 instances: 13 were given shortly after counter-singing near a territorial border; 6 while apparently foraging alone or with a fledgling nearby; 3 when near, leaving, or approaching an active nest; and 1 when my presence caused apparent alarm. The *zzee* call is probably the metallic call note described as a flight and contact call (Oliarnyk and Robertson 1996). (2) Both adults frequently gave long series of sweet, nonmetallic *chip* notes when I was near a nest containing nestlings or fledglings; in three cases, a female with a nest under construction engaged in extensive chipping when I was in the territory. (3) A high-pitched, nonmetallic alarm *tchip* was heard six times: twice from females, apparently alarmed by a nearby Turkey Vulture (*Cathartes aura*) or a female Brown-headed Cowbird (the latter near an active nest); once from a territorial male, apparently alarmed by a nearby Red-tailed Hawk (*Buteo jamaicensis*); and three times from three different females when I was near a nest with nestlings. (4) On 10 occasions, I heard territorial males—always accompanying a female with an active nest (eggs or young) or a nest under construction—give a series of very soft, almost warbled notes; apparently, this was the Cerulean War-

TABLE 1. Nest-tree and nest-location variables (mean ± SE) for Cerulean Warblers at Barry State Game Area (BSGA; *n* = 6 nests in 2003) and Fort Custer (FTCU; *n* = 12 nests in 2004, *n* = 18 nests in 2005). All values are in meters, except dbh (cm) and nest height/tree height (proportion). See methods for definitions of variables.

Site	Nest-tree dbh	Nest-tree height	Nest height	Nest height/ tree height	Distance to bole	Distance to foliage	Distance to gap
BSGA	45.5 ± 6.6	21.8 ± 2.0	18.7 ± 2.1	0.84 ± 0.04	3.5 ± 0.6	4.9 ± 1.9	17.7 ± 7.2
FTCU	38.1 ± 2.9	26.0 ± 1.1	19.0 ± 1.4	0.73 ± 0.04	3.8 ± 0.5	5.8 ± 1.1	1.5 ± 0.8
FTCU	41.9 ± 1.0	26.6 ± 4.0	20.1 ± 0.2	0.75 ± 0.37	4.1 ± 0.2	7.2 ± 0.4	2.9 ± 0.3

bler's whisper "song." I describe this vocalization as nonsong, as it differed strongly from the typical song.

Nest placement and tree species.—Nests usually were placed on a horizontal limb with a bifurcation immediately distal to the nest, but occasionally they were placed on a lateral branch in a cluster of small, upright shoots with leaves. One nest was inside a spherical mass of Virginia creeper (*Parthenocissus quinquefolia*) vines at the end of a short lateral branch. Mean nest-tree dbh exceeded 38 cm, and nest-tree height exceeded 21 m in all 3 years; at both sites, nest height averaged 19–20 m (Table 1). Trunk and foliage distances were essentially similar at the two sites, whereas gap distance differed strongly; nests tended to be found near roads (unpaved sand and gravel) at FTCU, but not at BSGA, where roads were fewer and narrower (Table 1). At BSGA, the closest gap for one nest was a dirt road, and for five nests the closest gaps were natural forest openings (one small marsh and four light gaps where trees had fallen, allowing light to reach the forest floor); at FTCU (years pooled), the closest gaps were roads (13 nests) and natural forest openings (apparently all light gaps; 17 nests). Nest height as a percentage of tree height was slightly greater at BSGA than at FTCU (Student's $t = 2.60$, $P = 0.014$, df = 32; Table 1). At BSGA, four tree species were used for nesting: black oak (*Q. velutina*; *n* = 3), northern red oak (*Q. rubra*; *n* = 1), white oak (*Q. alba*; *n* = 1), and black walnut (*n* = 1). At FTCU (years pooled), six tree species were used for nesting: black locust (*n* = 17), black walnut (*n* = 7), black cherry (*n* = 3), sugar maple (*Acer saccharum*; *n* = 1), and American sycamore (*Platanus occidentalis*; *n* = 1).

Male age.—Most males lacked a white supercilium (visible through binoculars) at BSGA (9 of 10), FTCU in 2004 (14 of 16), and FTCU in 2005 (16 of 20). The frequency distributions of the two male plumage types did not differ between sites in 2004 ($\chi^2 = 0.04$, df = 1, $P = 0.85$). Pooling all years, 84.8% (39 of 46) of males lacked a white supercilium. In 2005 at FTCU, 10 of the 14 males captured and aged in the hand were identified as ASY males, and 4 were identified as SY males.

Pairing, nest success, and brood parasitism.—Fifteen females were found on 23 territories at BSGA, and 19 females were found on 23 (2004) and 22 (2005) territories at FTCU. The relative frequency of paired and unpaired males did not differ between study sites (2003 versus 2004, $\chi^2 = 1.80$, df = 1, $P = 0.18$). Apparent nest success was 43% at BSGA and FTCU in 2004 and 52% at FTCU in 2005. (As most nests were high in the canopy, exact hatching dates could not be determined, and Mayfield estimates of nest survival could not be calculated.) At FTCU, two nests were found for each of three females in 2004, and two nests were found for each of four females in 2005, indicating renesting after nest failure; no confirmed renests were recorded at BSGA. Despite an appreciable rate of nest failure, the exact cause of nest failure could be determined for only 12 nests: 3 failed due to brood parasitism, (one cowbird young fledged in each case), 2 failed due to exposure (initial nest superstructure destroyed by heavy rain or nest branch broken off by high winds), and 7 failed due to predation. In the last case, the nest's rim was torn and/or the entire nest was tipped. In 2004, Cerulean Warbler pairs at BSGA and FTCU fledged 0.1 cowbird/breeding pair and 0.1 cowbird/nest; in 2005, warbler pairs at FTCU fledged 0.2 cowbird/breeding pair and 0.1 cowbird/nest.

In 23 territories intensively monitored at

BSGA in 2003, six nests and one recently fledged brood were found, and nine fledglings (3.0/successful nest) were produced. In 23 territories monitored at FTCU in 2004, 12 nests and 2 recently fledged broods were found, and 12 young fledged (2.0 per successful nest). In 22 territories monitored at FTCU in 2005, 19 nests and 6 recently fledged broods were found, and 30 fledglings (2.3 per successful nest) were produced.

Male reproductive success.—At BSGA, male reproductive success was 0.20 (all males) and 0.30 (paired males only) male fledglings/male. Corresponding values at FTCU were 0.26 and 0.32 male fledglings/male in 2004, and 0.68 and 0.79 in 2005. The number of fledglings/breeding pair was 0.60 at BSGA, and 0.63 (2004) and 1.58 (2005) at FTCU.

DISCUSSION

Nest placement.—As previous workers have found in other parts of the species' breeding range (Oliarnyk and Robertson 1996, Hamel 2000, Jones and Robertson 2001, Jones et al. 2001), Cerulean Warblers in Michigan chose a diversity of tree species for nest placement. Nests at BSGA and FTCU averaged 19–20 m in height; typical (pre-ice storm) nest height in a southern Ontario population was 11.6–11.8 m (Oliarnyk and Robertson 1996, Jones et al. 2001) and the range-wide mean nest height (excluding the present study) is 11.4 m (Hamel 2000). Nest height/nest-tree height of nests in the Ontario population (0.61) was lower than in southern Michigan (0.73–0.84). Thus, not only did Michigan Cerulean Warblers choose high nest sites, they also nested relatively high within a given nest tree. Given the intensive season-long nest searches conducted throughout all territories studied, it is unlikely that any low nests were missed.

Nonsong vocalizations.—The *zzee* call note appears multifunctional, as it was used by both sexes in a variety of situations. It was given more often by females, which apparently used the note as a contact call when they were at, or close to, the nest; the call may also function as an alarm note. Therefore, I used female *zzee* calls as cues for finding nests; when heard, I attempted to watch the female return to an active nest, or to find the nest if the call was thought to have been given by a sitting female. The relatively few occurrences of male *zzees* were nearly all associated with active territorial defense against a nearby rival male, but several were given near an active nest. The sweet *chip* notes—given in response to my presence near nests containing older nestlings or fledglings—were alarm notes generally resembling the alarm chips of other North American parulids (Getty 1993). The higher-pitched *tchip* alarm note was rarely heard, and only in response to either a potential predator, a cowbird near the nest, or my presence in the territory. I heard the whisper "song" 10 times, all in the context of a male interacting with a female near an active nest. Intersexual behavior was difficult to observe, as birds generally remained high in the forest canopy, but males may give this vocalization as a "song cue" to nesting females (Barg 2002).

Male age.—Cerulean Warbler males with a white supercilium (SY males, Dunn and Garrett 1997) composed 10–20% of all territorial males at my study sites. Only 4 of the 14 banded males in 2005 were in the SY age class. Although aging by supercilium alone is, at best, an approximation, general agreement between the two aging methods used suggests that a significant majority of the breeding territorial males were in their second or a subsequent breeding season. In southern Ontario, 15% of males are thought to be SY birds (Jones et al. 2004). Thus, at least two populations in the northern part of the breeding range are biased toward older males. The two southwestern Michigan populations I studied are approximately 774 km from the southern Ontario study site. Within the range of another *Dendroica* species, the Black-throated Blue Warbler (*D. caerulescens*), Graves (1997) found latitudinal segregation among males, by age class. Furthermore, first-year American Redstart (*Setophaga ruticilla*) males are forced into marginal breeding habitat by older males (Ficken and Ficken 1967, Sherry and Holmes 1989). Further field study is required to investigate possible habitat-specificity and/or broader geographical extent of age-structured breeding populations of Cerulean Warblers.

Population productivity.—Excluding unpaired males, male reproductive success was 0.30–0.32 male fledglings/breeding male at

BSGA (2003) and FTCU (2004) and 0.79 male fledglings/breeding male at FTCU (2005). Reproductive output in southwestern Michigan was, therefore, poor in two distinct habitat types in 2 of 3 years, and in all 3 years it was lower than the productivity of a southern Ontario population (0.94 male fledglings/breeding male)—thought to be a sink population requiring 1.7 male fledglings/breeding male for sustainability (Jones et al. 2004). Survival estimates for the Michigan study populations are needed, however, before determining whether they are self-sustaining or not.

A previous study of passerine populations in southwestern Michigan (Rogers and Caro 1998) indicated that corvid nest predators (American Crow, *Corvus brachyrhynchos*; Blue Jay, *Cyanocitta cristata*) and brood parasites (Brown-headed Cowbird) are regular inhabitants of all habitat types, including the interior of large forest tracts, as well as suburban, exurban, and agricultural areas. Avian nest predators and cowbirds were frequently observed in both forest edge and interior on annual point counts from 1993 to 2004 (CMR unpubl. data). Corvids, therefore, are candidates for causing nest failure in Cerulean Warblers at BSGA and FTCU. Nest predation also may have been caused by eastern fox squirrels (*Sciurus niger*), which were common at both study sites, and eastern chipmunks (*Tamias striatus*), which were abundant at BSGA. Both sciurid species were observed in trees at heights exceeding 10 m. Effects of cowbird parasitism were low in all 3 years; however, >60% of the Hooded Warbler (*Wilsonia citrina*) nests at FTCU were parasitized by cowbirds in 2004–2005 (R. Adams pers. comm.). The Cerulean Warbler's status as a poor cowbird host deserves further attention.

A possible source of error in my study was the failure to detect fledglings in all territories. Although this cannot be completely discounted, any error was probably negligible, as Cerulean Warbler adults feeding older nestlings or fledglings typically became excited, and gave frequent and obvious alarm calls (*chips*); in addition, all fledged broods and adults (of all species) emitting alarm-chips were identified to species. It is unlikely that enough fledglings were missed to bias my estimates of (low) reproductive output. Some territories yielded no fledglings for an entire breeding season. This is not necessarily surprising, as the breeding season is short: no July nest starts were found in 2 years, and the species begins breeding after spring migration in mid-May. At BSGA in 2003, females were not detected on 8 of 23 territories (35%); thus, some females may have been missed. However, Holmes et al. (1996) found a similar percentage (27%) of unpaired males among Black-throated Blue Warblers.

Low reproductive output among Cerulean Warblers may be a factor contributing to their long-term population decline. To test this hypothesis more rigorously, additional studies of this species are needed. Specifically, reproductive output should be measured in more regions. In addition, longer-term studies would be useful for assessing temporal variation in reproduction within individual sites. Finally, age structure strongly biased toward older males suggests a need for regional, as opposed to local, models of the Cerulean Warbler's population dynamics.

ACKNOWLEDGMENTS

The able field assistance of staff members of the Kalamazoo Nature Center is gratefully acknowledged, particularly that of B. Nelson, who captured and aged male Cerulean Warblers. The U.S. Army Fort Custer Reserve unit and the Michigan Department of Natural Resources kindly permitted access to the study sites, and Kellogg Biological Station provided important logistical support. J. Jones and two anonymous referees provided useful comments on an earlier version of the manuscript. This is contribution number 1210 of Kellogg Biological Station.

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The Wilson Journal of Ornithology 118(2):152–163, 2006

MIGRANT SHOREBIRD PREDATION ON BENTHIC INVERTEBRATES ALONG THE ILLINOIS RIVER, ILLINOIS

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ABSTRACT.—We evaluated the effect of shorebird predation on invertebrates at a wetland complex along the Illinois River, west-central Illinois, during spring migration. Using a new exclosure experiment design adapted to the shifting nature of foraging microhabitat of interior wetlands, we found that shorebird predation did not significantly deplete total invertebrate density or total biomass in open (no exclosure) versus exclosure treatments. Chironomids and oligochaetes were the most common invertebrates occurring in substrate samples. The density of oligochaetes was lower in open treatments, though the degree of difference varied both spatially and temporally. Shorebird density was positively correlated with the amount of invertebrate biomass removed from the substrate during the late-May sampling period. Our results suggest that shorebirds use an opportunistic foraging strategy and consume the most abundant invertebrate prey. The dynamic hydrology at our study site likely played a role in preventing invertebrate depletion by continually exposing new foraging areas and prey. *Received 16 February 2005, accepted 30 December 2005.*

Migrating shorebirds (Charadriiformes) require stopover resources for rest and rapid accumulation of energy to fuel their transcontinental migration (Myers et al. 1987). As freshwater wetlands in the United States continue to be converted to agriculture and development (Dahl 2000), the reduction in stopover areas is believed to have negative effects on shorebird populations (Sutherland and Goss-Custard 1991, Harrington et al. 2002). Consequently, many North American shorebirds are listed as threatened, endangered, or species of special concern (Brown et al. 2001, Morrison et al. 2001), including Greater Yellowlegs (*Tringa melanoleuca*), Short-billed Dowitcher (*Limnodromus griseus*), and Buff-breasted Sandpiper (*Tryngites subruficollis*) in the Mississippi Alluvial Valley and Great Lakes region.

While migrating through the interior United States, shorebirds are faced with unpredictable habitats that are much different from coastal systems (Skagen and Knopf 1994a). The predictability of tidal cycles and blooms of food resources in the intertidal zones of coastal systems support large concentrations of shorebirds and high levels of site fidelity in locations such as Delaware Bay along the northeast Atlantic coast and the Copper River Delta in the Gulf of Alaska. In contrast, shorebirds using interior flyways are more dispersed and occur at stopover habitats in smaller numbers than those using coastal flyways (Skagen and Knopf 1993). Some shorebirds undertake long, nonstop flights; many other species do not depart with enough fuel to reach their final destinations and must make multiple stops to refuel during migration (White and Mitchell 1990, Skagen and Knopf 1994b, Farmer and Wiens 1999)—a less energetically challenging strategy (Piersma 1987).

Shorebirds are opportunistic feeders and readily shift their diet to exploit locally abundant invertebrate resources (Skagen and Oman 1996). Studies of shorebird diet among interior stopover habitats indicate that chironomid larvae are the dominant prey items (Helmers 1991, Mihue et al. 1997). Much less is known about the importance of oligochaetes—often the most abundant invertebrates in freshwater mudflats in the Mississippi Alluvial Valley (Elliott-Smith 2003, Hamer 2004, Mitchell and Grubaugh 2005)—as prey (Safran et al.

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1997). The importance of oligochaetes may be underestimated because they are small, fragile, sensitive to post-mortem digestion in esophageal, proventricular, and gizzard contents, and are thus often ignored in analysis (Rundle 1982, Safran et al. 1997). However, oligochaetes are comparable to chironomids in caloric value (5,575 and 5,424 calories/g dry weight, respectively), crude protein, and gross energy (Cummins and Wuycheck 1971, Anderson and Smith 1998).

Observational studies, esophageal analyses, and exclosure experiments have been used to assess the interactions between shorebirds and their prey (Brooks 1967, Schneider 1978, Evans et al. 1979, Rundle 1982, Swennen 1990). Food consumption has been measured using indirect visual methods in many studies of the foraging ecology of Palearctic, coastal shorebirds (Evans et al. 1979, Moreira 1997). These indirect methods, however, are often challenging to use in inland systems where prey are small and successful and unsuccessful foraging pecks and probes are not distinguishable. Collecting individual shorebirds for esophageal analysis provides valuable information on diet, but it does not determine the effect of shorebird predation on the invertebrate community and may produce bias caused by missing soft-bodied invertebrates (Rundle 1982). A less invasive technique for investigating shorebird-prey relationships is to use exclosure experiments, also termed caging experiments, which entail structures that prevent shorebirds from feeding on invertebrates within the enclosed substrate. The invertebrate community within the exclosure can be compared with that in equivalent substrate outside the exclosure for an indirect measure of shorebird predation on invertebrates.

Recently, researchers have implemented exclosure experiments at freshwater shorebird stopover sites (Mihue et al. 1997, Ashley 2000, Mitchell and Grubaugh 2005), but previously the majority had been conducted in marine intertidal systems (Wilson 1991, Mercier and McNeil 1994, Weber and Haig 1997). Results of these exclosure experiments are varied; some studies have revealed up to 90% reductions in prey densities due to shorebird predation (Schneider and Harrington 1981, Szekely and Bamberger 1992), whereas other studies document no measurable effect (Raffaelli and Milne 1987, Mitchell and Grubaugh 2005). During migration in the interior flyways, the extent of shorebird predation on different invertebrate taxa at stopover areas is not clear.

We conducted an exclosure experiment at a shorebird stopover location in the Upper Mississippi Alluvial Valley. Our primary objectives were to evaluate (1) whether shorebird predation depletes invertebrate prey during migration along an interior flyway, (2) which invertebrates and size classes are removed from the substrate, (3) the chronology in abundance and biomass of benthic invertebrates, and (4) a new exclosure-experiment design adapted to the unpredictable nature of interior shorebird foraging habitats.

METHODS

Study area.—Our study was conducted at Chautauqua National Wildlife Refuge (NWR) (40° 38′ N, 89° 99′ W) and Emiquon NWR (40° 32′ N, 90° 09′ W), which are part of a large wetland complex along the Illinois River in west-central Illinois near Havana (Fig. 1A). The 1,816-ha refuge at Chautauqua NWR was established in 1936 and consists of large backwater lakes, and bottomland and upland forest. Chautauqua also has been designated a stopover of international importance by the Western Hemisphere Shorebird Reserve Network (Harrington and Perry 1995). The late drawdown in July and August at this refuge creates extensive, shallow-water mudflats attracting an estimated 100,000 to 250,000 shorebirds each fall (Bailey 2003). Comparatively little shorebird habitat is available at Chautauqua in the spring, when water levels are elevated to prevent encroachment of exotic invasives—black willow (*Salix nigra*) and cocklebur (*Xanthium strumarium*)—that interfere with moist-soil plant production.

Emiquon NWR is an 856-ha refuge composed of backwater lakes, sloughs, forested wetlands, and a variety of other terrestrial habitats. Because Emiquon was only just acquired in 1993, much of the refuge comprises newly established wetland, and portions will remain in agriculture until leases with private landowners expire. The refuge is divided into two main units: Wilder Tract (197 ha) and South Globe (288 ha). The Wilder Tract was taken out of agricultural production in 1998 and is

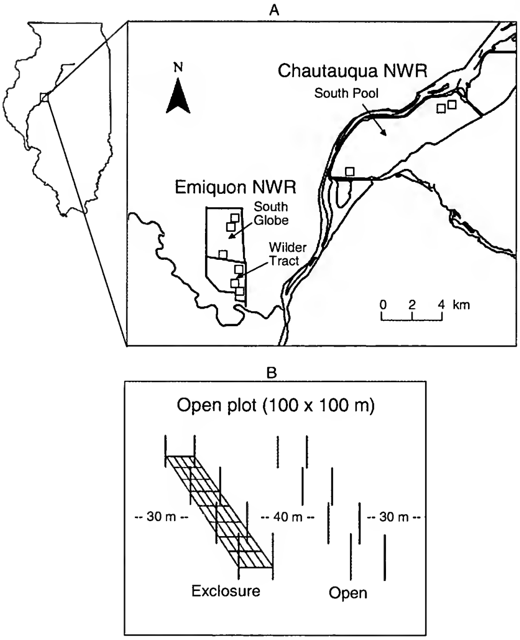

FIG. 1. (A) Location of the three study sites near Havana, Illinois (Chautauqua South Pool, Emiquon South Globe, Emiquon Wilder Tract) where shorebird predation was studied from February to June 2004. White squares show approximate location of study plots. (B) Depiction of a plot (1 ha) containing one exclosure and one open (no exclosure) treatment used in this study. The dashed lines indicate approximate location of the shoreline (mud/water interface where shorebirds foraged).

managed as a moist-soil unit. The South Globe unit was taken out of production for the first time in 2004, when the remaining corn and bean stubble were flooded to create extensive shallow water habitat.

Field methods.—The exclosure experiment was conducted during spring shorebird migration from March through June 2004. Three plots were established at each of the three field sites (Chautauqua South Pool, Emiquon Wilder Tract, Emiquon South Globe) for a total of nine plots (Fig. 1A). Each plot was 1 ha in size (100 × 100 m, designated by flags at each corner) and contained both an exclosure treatment and an open treatment. The exclosure consisted of a sheet (16 × 1 m) of metal fencing (mesh = 5 × 10 cm) positioned horizontally and supported 10 cm above the substrate by metal stakes at each corner and at 5-m intervals along both sides (Fig. 1B). The long axis of the exclosure was placed perpendicular to the shoreline so that the shoreline always remained within some part of the exclosure as water levels fluctuated. Because the fence sagged between the metal stakes, small sections of black willow branches were used to prop up the fence to maintain the entire unit at a 10-cm height. Few predators of benthic invertebrates—other than shorebirds, largely predatory invertebrates, and crayfish—occur in this inland system. The lack of sides on the exclosure, however, allowed access by other predators and excluded only avian predators. The open treatment lacked any fencing but was marked by flags to the same dimensions of the exclosure. The open and exclosure treatments were placed 40 m apart and 30 m from the edges of the plot (Fig. 1B). Because of the changing hydrology and changing locations of shorebird habitat, plots were not established at the same time. The first plot was established on 27 February and the last on 29 April.

We determined shorebird use of the plots by conducting censuses twice per week at each plot during the peak of migration (mid-April to the end of May) and once per week during the remainder of spring migration. Means were calculated for each 2-week period for each plot to determine average shorebird density in the 2-week period before invertebrate sampling. The first survey was on 6 March and the last was on 16 June. During each census, we identified and counted all shorebirds in the 1-ha plot (from a vehicle or on foot) using 8 × 42 binoculars or a 15–45× spotting scope. We recorded water levels during each census using a PVC pipe (vertical pole) marked at 1-cm intervals; a pole was placed permanently outside each plot in water that was deeper than it was inside the plot. We determined change in water level by comparing the water level from each 2-week sampling period at each plot. The absolute value of the change in water level was used in the analysis.

We sampled for benthic invertebrates in both treatments when each plot was established and then at 2-week intervals throughout spring migration. The first samples were taken on 27 February and the last on 6 June. Each treatment was sampled at the shoreline (where edge of surface water meets mudflat), which was the primary shorebird foraging zone.

Only one core sample per 2-week interval was taken from each treatment to avoid potential resampling of the same area in subsequent sampling periods and to avoid sediment disturbance. Ashley et al. (2000) conducted a study in which two cores were sampled in each treatment; they found no difference between the subsamples and recommended eliminating them in future exclosure studies. We used core samplers, similar to those developed by Swanson (1978), that were modified by using metal conduit piping with a sharpened edge. We extracted core samples 5 cm in diameter to a depth of 5 cm (Sherfy et al. 2000). After inserting the core sampler into the substrate, we placed a plumber's stopper plug in the end of the core sampler to aid in removal of the core. Contents of the sampler were placed in a resealable plastic bag containing 95% ethyl alcohol, stained with Rose Bengal, and kept cool until sorted.

Laboratory methods.—Invertebrates were removed from the preserved sample using a number 30 mesh sieve and identified to order or family according to Pennak (1989) and Merritt and Cummins (1996). All samples were sorted by one observer to reduce bias. Chironomids and gastropods were sorted into two size classes: ≤ 5 mm and >5 mm. All invertebrates, excluding gastropods, were dried at 70° C for 24 hr on pre-dried and preweighed glass microfiber filters. To determine biomass, we weighed samples to the nearest 0.0001 g using a Mettler balance. Invertebrate densities (no. individuals) and biomasses (g) are reported per m^2.

Statistical analysis.—To determine whether differences existed between the two treatments prior to the experiment, we used paired *t*-tests to compare measures of invertebrate density and biomass before we established the plots. To analyze invertebrate density and biomass, we used a repeated measures mixed-model analysis of variance using PROC MIXED (Littell et al. 1998, Sherfy and Kirkpatrick 2003) in SAS 8.0 (SAS Institute, Inc. 2000). Fixed factors in the model included sampling period, site, predation, and all two-way and three-way interactions. Predation (defined as the number of invertebrates removed) was determined by subtracting the values for invertebrates in the open treatment from values for invertebrates in the exclosure treatment, for each pair. Values above zero indicate greater invertebrate densities in the exclosures, suggesting that shorebirds removed invertebrates from outside the exclosure treatment. The random factor of plot (site) was included as an error term in the model; site represents the main blocking factor. To avoid problems with different initiation dates for the plots, we used samples only from early May, late May, and early June in the PROC MIXED analysis, which matched the timing of shorebird migration. We also included shorebird density ($\log_{10}$ [X + 1]-transformed) and change in water level as covariates in the model.

A separate analysis was performed for all eight invertebrate density (individuals/m^2) variables (oligochaete, total chironomid, small chironomid, large chironomid, total gastropod, small gastropod, large gastropod, total invertebrate) and for invertebrate biomass (g/m^2). Data on large chironomids included many zero values that resulted in an infinite likelihood error; therefore, they are not reported. To meet assumptions of normality, we transformed all invertebrate data ($\log_{10}$ [X + 1]) prior to analysis.

PROC MIXED allows specification of the covariance structure of the R matrix (Littell et al. 2000). We used the compound-symmetry structure, which has constant variance and covariance between repeated measures and assumes that all repeated measures on a subject (i.e., plots) are equally correlated regardless of their temporal relationship. We used linear regression to analyze correlations between shorebird density and invertebrate density, and between shorebird density and biomass removed, in the nine plots for the early May and late May sampling periods. Statistical significance was set at $P < 0.05$ and all means are presented ± SE.

RESULTS

We found no difference in oligochaete density ($t = 0.25$, df = 15, $P = 0.81$) or invertebrate biomass ($t = 0.02$, df = 15, $P = 0.98$) between the exclosure and open treatments from the initial samples taken just before the plots were established. Differences in chironomid density ($t = 2.15$, df = 15, $P = 0.048$) and invertebrate density ($t = 2.22$, df = 15, $P = 0.043$) between the exclosure and open treatment indicated a heterogeneous invertebrate community at the onset of the experiment.

We conducted 116 shorebird surveys and observed 15 shorebird and 11 waterfowl species foraging inside the plots. We observed 838 shorebirds, 89% of which consisted of Least Sandpiper (*Calidris minutilla*; $n = 309$), Pectoral Sandpiper (*Calidris melanotos*; $n = 268$), Lesser Yellowlegs (*Tringa flavipes*; $n = 118$), and Killdeer (*Charadrius vociferus*; $n = 49$). We observed 463 waterfowl, 94% of which were Green-winged Teal (*Anas crecca*; $n = 145$), Northern Shoveler (*A. clypeata*; $n = 110$), Blue-winged Teal (*A. discors*; $n = 105$), and Mallard (*A. platyrhynchos*; $n = 76$). During the early-May to early-June sampling periods used in the PROC MIXED analysis, only 22 waterfowl and 677 shorebirds were observed in the plots. Mean shorebird density across all sites from late March to early June was 6.3/ha ± 1.5 ($n = 36$); peak density occurred in early May (12.3/ha ± 2.8, $n = 9$; Fig. 2). The highest shorebird density (39.8/ha) occurred at Chautauqua on 20 May.

We collected 108 benthic core samples, but not all of these were used in the analysis due to the dynamic hydrology. Oligochaete density (all sites combined) from late March to early June was 15,137.5/m^2 ± 3,005.1 in exclosure treatments ($n = 36$; Fig. 2) versus 11,798.8/m^2 ± 3,131.4 ($n = 36$) in open treatments. Chironomid density was 2,291.9/m^2 ± 461.1 ($n = 36$) in exclosure treatments and 2,306.0/m^2 ± 573.0 ($n = 36$) in open treatments. Oligochaete density peaked in late May (22,975.1/m^2 ± 8,999.8; $n = 36$) and chironomid density peaked in early May (5,715.5/m^2 ± 1,548.5; $n = 36$). The greatest oligochaete density observed in a single sample occurred on 20 May in an open treatment at Emiquon Wilder Tract (88,618.2/m^2), and the greatest chironomid density was recorded on 7 May from the same site (16,297.6/m^2).

Oligochaete density ($F_{1,26} = 7.20$, $P = 0.013$) and large gastropod density ($F_{1,26} = 0.21$, $P = 0.049$) differed between treatments, indicating a significant predation effect (Table 1); a significant predation × period × site interaction for oligochaetes indicated that the effect varied both spatially and temporally ($F_{4,26} = 3.19$, $P = 0.029$). The grand mean for oligochaete density was 1.2× greater in the exclosure than in the open treatments. Based on the total of mean invertebrate densities for all the plots, shorebirds removed 18.9% of the total invertebrates from the substrate. Density of chironomids, total invertebrate density, and total invertebrate biomass did not differ between treatments.

Mean change in water level (all sites combined) was 10.33 ± 2.23 cm ($n = 36$). The change in water level influenced only oligochaete density ($F_{1,26} = 4.45$, $P = 0.045$); shorebird density had no influence on any response variables (Table 1). Shorebird density was positively correlated with invertebrate biomass removed ($r^2 = 0.64$, $P = 0.010$) and invertebrate density removed ($r^2 = 0.39$, $P = 0.071$) in late May (Fig. 3). Chautauqua contributed the most to the positive correlation between shorebird density and invertebrate biomass removed.

DISCUSSION

Exclosure design.—A concern with exclosure experiments in soft sediments is the presence of artifacts produced by the exclosure structure (Virnstein 1978). Many of these artifacts, however, are associated with marine intertidal systems, where the influences of exclosure structure appear greater than in nonintertidal systems. Hulberg and Oliver (1980) found that exclosures alter the level of sedimentation, which in turn influences populations of polychaetes. Their study was performed on a wave-exposed coastal beach that is a very different environment from our system, which lacked wave perturbations and a diurnal tide. Quammen (1981) established an exclosure design to separate the effects of multiple predators within a system: a floating exclosure without sides prevented access by shorebirds while allowing fish to enter the exclosure during high tide. This design, however, is not as appropriate for a system without tides and with fewer predators of benthic invertebrates. Although common carp (*Cyprinus carpio*) were observed in our impoundments, no fish were observed foraging at the soil/water interface where core samples were taken. Even if other predators of benthic invertebrates went unnoticed, the lack of sides on our exclosure should have allowed normal access. We also had no evidence that the exclosure

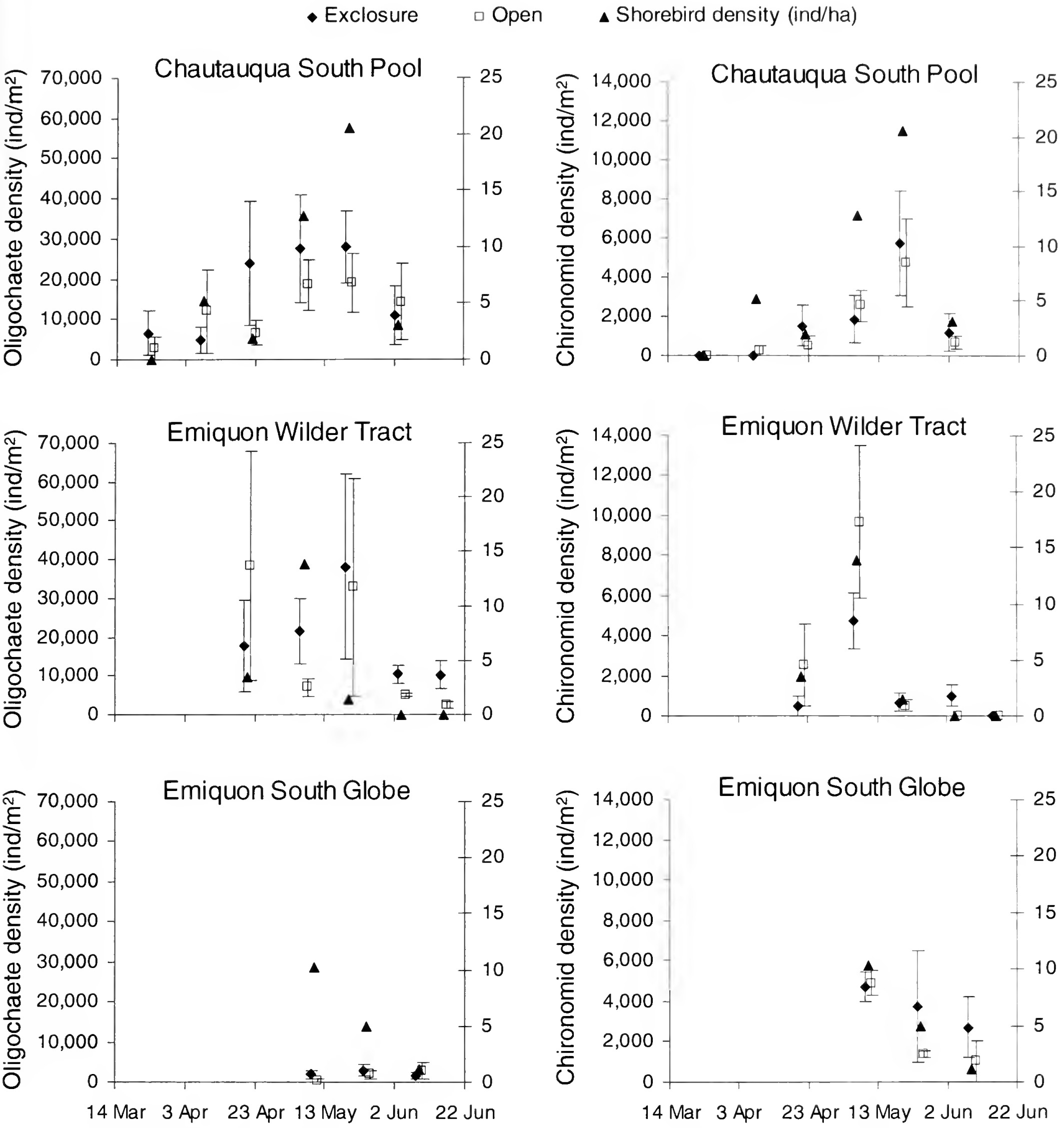

FIG. 2. Mean density of oligochaetes and chironomids (mean ± SE) in exclosure and open (no exclosure) treatments at three study sites: Chautauqua South Pool ($n = 15$), Emiquon Wilder Tract ($n = 12$), and Emiquon South Globe ($n = 9$) in Havana, Illinois, from late March to early June 2004. Shorebird density (filled triangles; individuals/ha; $n = 36$) shown without error bars for clarity.

represented either shelter or obstruction for larger predators, such as crayfish.

A potential problem with exclosure experiments is the build-up of algae on the cage structure (Virnstein 1978). Algae grew on several of our exclosures, but only where the fence was immersed in deeper water (>10 cm), and algae were never present at the sampling locations. If water levels had dropped quickly at an exclosure with algal growth, the physical nature of the soil/water interface could have been influenced; however, this did not occur during our study.

Exclosure structures are often used as avian roosts, which could influence the nutrient levels in the exclosure through the addition of feces. Weber and Haig (1997) reduced tern and gull roosting on wooden stakes by sharp-

TABLE 1. Results of repeated measures mixed-model analysis of variance for shorebird predation effects on invertebrate density (individuals/m^2) and biomass (g/m^2) in mudflats at Chautauqua and Emiquon NWR near Havana, Illinois, during early May, late May, and early June, 2004.

		Oligochaete density		Total chironomid density		Small chironomid density	
Effect	df	*F*	*P*	*F*	*P*	*F*	*P*
Site	2,6	0.05	0.95	2.44	0.17	1.08	0.40
Period	2,11	0.89	0.44	5.69	0.020	3.47	0.068
Period × Site	4,11	2.40	0.11	1.20	0.37	0.63	0.65
Predation	1,26	7.20	0.013	0.08	0.79	0.00	0.97
Predation × Site	2,26	5.20	0.013	0.06	0.95	0.22	0.80
Predation × Period	2,26	4.47	0.022	0.15	0.86	0.08	0.92
Predation × Period × Site	4,26	3.19	0.029	1.09	0.38	0.62	0.65
Shorebird density	1,26	0.00	0.98	1.20	0.28	0.61	0.44
Change in water level	1,26	4.45	0.045	1.09	0.31	0.42	0.52

[a] Indicates mixed-model error to an infinite likelihood from too many zero values in the data.

ening their ends. Our metal stakes were occasionally used as roosts by Red-Winged Blackbirds (*Agelaius phoeniceus*), and feces at the base of some stakes were present in small amounts. Core samples, however, were taken from the middle of the exclosure and the open treatments, thus avoiding the base of stakes by at least 0.5 m.

Interior freshwater wetlands are challenging environments for exclosure experiments because of their unpredictable hydrology. The zone of shorebird foraging habitat constantly shifts as water levels fluctuate. The exclosure design commonly used in marine intertidal systems consists of 1-m^2 treatments, which is not appropriate in an interior system because the exclosure would not be long enough to ensure that the fluctuating shoreline foraging zone would always remain within the exclosure. Mitchell and Grubaugh (2005) used the traditional square exclosure design and established 113 plots in the Lower Mississippi Alluvial Valley. The plots were repeatedly sampled over the course of two summer/fall migrations, but only the plots representing shorebird foraging habitat (wet substrate or water depth <10 cm) were sampled. As a result, many plots were never sampled during their study. Our new design was implemented to compensate for the dynamic hydrology by establishing each treatment as a linear transect perpendicular to the shoreline. This allowed repeated sampling as water levels changed throughout the migration period. However, even with this modified design, only 9 of 16 plots originally established were used in our study; the water level changed so dramatically in the other 7 plots that the shoreline did not remain within the treatments.

When the height of the exclosure structures was maintained at 10 cm above the substrate, prevention of shorebird predation was accomplished. On two occasions, however, we found evidence that shorebirds had been inside the exclosure (presence of tracks and feces). This occurred when the fence sagged below 5 cm (shorebirds walked over the fence), or was above 15 cm (shorebirds walked under fence).

We believe that the only major factor accounting for differences in the response variables (e.g., invertebrate density) between the two treatments was the exclusion of avian predators. We observed 22 waterfowl and 677 shorebirds inside plots during the sampling period used in the analysis. Most of the waterfowl observed foraged in deeper water and likely did not influence the benthic invertebrates at the shoreline. Therefore, most differences between the treatments were likely attributed to shorebird predation.

Exclosure experiments continue to be valuable tools for studying predator-prey interactions. Future studies in non-intertidal, soft sediments may benefit from implementation of an experimental design similar to the one used in this study. Researchers are well aware of exclosure artifacts in marine systems, but little is known about the influences of exclosure structures in interior wetlands. A third treatment (in addition to the exclosure and open control) used in many marine studies is the use of a "cage control" that has a top

TABLE 1. Extended.

Total gastropod density		Small gastropod density		Large gastropod density		Invertebrate density		Invertebrate biomass	
F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
1.23	0.36	0.84	0.48	1.01	0.42	0.42	0.68	0.43	0.67
3.34	0.073	2.18	0.16	0.14	0.87	0.51	0.61	2.79	0.10
2.63	0.092	3.09	0.062	0.66	0.63	1.47	0.28	1.23	0.35
0.26	0.62	0.02	0.90	4.21	0.049	0.32	0.58	1.20	0.28
6.76	0.014	3.32	0.049	1.20	0.31	1.29	0.29	0.01	0.99
5.65	0.024	1.17	0.29	1.77	0.19	0.31	0.74	2.34	0.12
—[a]	—	—	—	—	—	1.18	0.34	2.35	0.081
0.17	0.68	0.40	0.53	0.14	0.71	0.17	0.69	0.86	0.36
0.39	0.54	0.34	0.56	0.11	0.75	0.32	0.58	0.26	0.62

cover and two sides, which is designed to identify the effects of the cage structure while allowing normal predation to occur (fish or crabs could enter the cage from the two open sides). The presence of the exclosure cover, however, is likely to influence normal shorebird foraging. Weber (1994) attempted to account for this effect by establishing a cage control identical to the exclosure treatment but without the cover, which evaluated the influence of the stakes but not the potential effects of the exclosure cover.

Predator–prey interactions.—Our results indicate that migrating shorebirds did not locally deplete invertebrate populations at our study sites, and only oligochaete density was reduced by shorebird foraging. We were surprised to find that shorebirds affected oligochaete densities, but not chironomid densities. Chironomids are known to be important shorebird prey throughout interior stopover locations (Eldridge 1987, Helmers 1991, Skagen and Omen 1996, Mihue et al. 1997), but our results suggest that shorebirds did not select chironomids over other prey. Oligochaetes are often the most abundant freshwater invertebrate in mudflats in the Mississippi Alluvial Valley (Elliott-Smith 2003, Mitchell and Grubaugh 2005), and they were the most abundant prey at our study sites (Hamer 2004). Our results support Skagen and Omen's (1996) assertion that dietary flexibility allows shorebirds to exploit variable resources. The effect of shorebird predation varied spatially, and we identified at least four factors that could have influenced shorebird predation pressure on benthic invertebrates.

First, the energy demands of shorebirds are highly variable. Different intensities of shorebird predation occurring seasonally on the coast of Venezuela were explained by the different energy demands of molt, fat deposition, and foraging habitat (Mercier and McNeil 1994). Wilson (1991) compared episodic shorebird predation at the Bay of Fundy, Nova Scotia, and at Grays Harbor, Washington, and found a significant reduction of major prey at the Bay of Fundy but no effects of predator exclusion at Grays Harbor. The difference in the intensity of predation was explained by differing migration strategies at these two sites. Shorebirds using Grays Harbor tend to migrate in short hops (Iverson et al. 1996, Warnock and Bishop 1998) and do not need to accumulate the massive fat reserves required for a transoceanic migration strategy like shorebirds departing from the Bay of Fundy. The short hop migration strategy of interior shorebirds (Skagen and Knopf 1994b, Farmer and Wiens 1999) may explain why other studies of shorebird predation in the interior U.S. also show little effect of predator exclusion on invertebrate prey (Mihue et al. 1997, Ashley et al. 2000, Mitchell and Grubaugh 2005). Multiple stops reduce the need to accumulate large amounts of fuel at one location.

Second, shorebird territoriality may influence the degree of episodic predation on invertebrates. As shorebird densities increase,

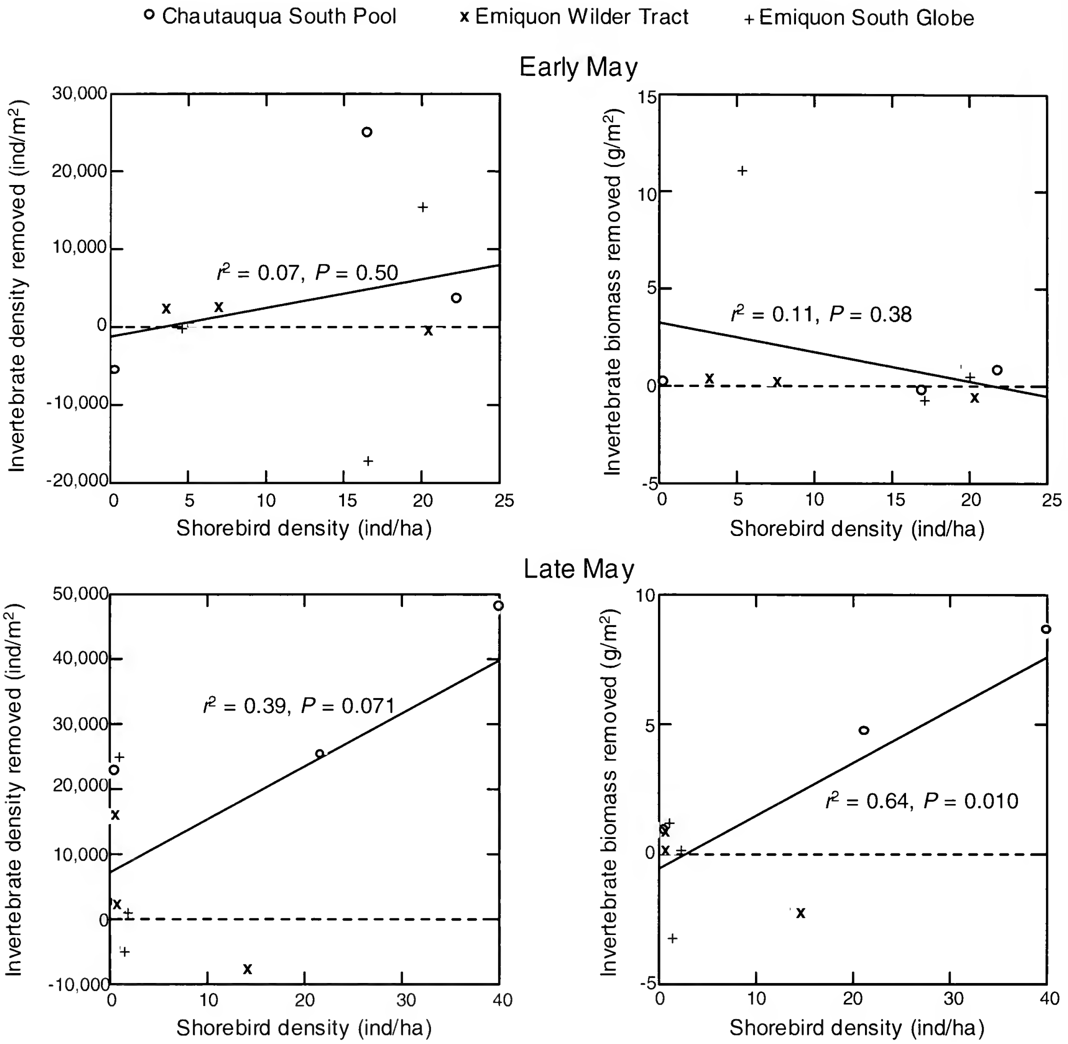

FIG. 3. Relationship between invertebrate biomass removed (g/m^2) and density removed (individuals/m^2) versus shorebird densities (individuals/ha) at Chautauqua South Pool, Emiquon South Globe, and Emiquon Wilder Tract near Havana, Illinois, in early May and late May of 2004. Values for biomass and density removed were calculated by subtracting open from exclosure values. A value of zero (dashed line) represents equal biomass (or density) in the exclosure and open treatments. Values >0 indicate greater biomass (or density) in the exclosure. Note difference in scales.

interference (fighting, kleptoparasitism, disturbance) between territorial birds limits the depletion of resources (Goss-Custard 1980). Duffy et al. (1981) studied shorebird competition for prey resources at a wintering ground in Peru and did not find depletion of invertebrate prey; one factor reducing the importance of competition may have been territoriality among the wintering birds. Migrant shorebirds at our stopover location are mostly nonterritorial (Hamer 2004); thus, territorial interactions likely did not play a role in the shorebird/prey dynamics at our study sites.

Third, shorebird predation pressure is greater in locations with greater densities of foraging birds. Shorebird densities observed during our study averaged 6.3/ha, peaking at 39.8/ha. Coastal flyways receive much greater concentrations of shorebirds where densities can approach 100/ha (in coastal South Carolina; Weber and Haig 1997) to 4,500/ha (in coastal Venezuela; Mercier and McNeil 1994).

The dispersed migration through interior habitats results in lower shorebird densities and possibly reduces predation pressure.

Finally, the dynamic water levels recorded during our study may have been an additional factor that reduced the effect of shorebird predation on benthic invertebrates. Water levels fluctuated an average of 8.9 cm during 2-week intervals. Gradual drawdown or flooding continuously shifts the location of foraging habitat and exposes new invertebrate prey (Rundle and Fredrickson 1981). Even though managers at Chautauqua's South Pool attempted to maintain a stable water level over the course of the spring, the average fluctuation over each 2-week period was 7.6 cm. Much of this variation can be explained by wind-driven seiches (wind fetch), which can expose previously unexploited foraging habitat in large, shallow wetlands (Laubhan and Fredrickson 1993). Without this phenomenon, shorebird reduction of invertebrates at Chautauqua may have been greater.

Because shorebirds are size-selective when preying on invertebrates, they can influence the invertebrate community structure in soft sediments (Peterson 1979, Kent and Day 1983, Wilson 1989). Shorebird predation on marine polychaetes often targets large (adult) individuals, which can lead to increased recruitment of juveniles and increased densities of smaller invertebrates. As a consequence, exclosure experiments in which only prey densities are measured may fail to account for the interactions of size-class predation and size-dependent competition. Our results, however, do not suggest that such episodic shorebird predation influenced the invertebrate community structure in our study. There was no evidence of size-selection of chironomids, but the mean density of large gastropods was more than seven times greater in the exclosure than the open treatment (106.1/m^2 versus 14.1/m^2, respectively). Thus, it seems likely that shorebirds selected large gastropods, which has been observed elsewhere in the Mississippi Alluvial Valley (Brooks 1967, Rundle 1982).

Competition for prey resources at migration stopover locations may result when early migrants deplete prey resources and reduce the successful foraging rate of later-arriving shorebirds, thus increasing the length of stay for later arrivals (Wilson 1991). Although this occurs at some locations (Schneider and Harrington 1981), later migrants at our study site were not likely disadvantaged by reductions in prey density by early migrants because the dynamic hydrology constantly exposed previously unexploited food resources.

Our results suggest that migrating shorebirds along the Illinois River may have reduced oligochaetes and larger gastropods. Flexible and opportunistic foraging strategies are beneficial to shorebirds facing the unpredictable nature of interior flyways. The removal of oligochaetes, the most abundant invertebrates at our study sites, suggests that shorebirds fed opportunistically on the most available prey. The dynamic hydrology, and the resulting continuously renewing availability of invertebrate prey, likely offer sufficient invertebrate resources for migrating shorebirds in the Illinois River valley.

ACKNOWLEDGMENTS

This research, conducted as part of a master's thesis, was funded by the Illinois Natural History Survey, the Illinois Department of Natural Resources Wildlife Preservation Fund, The Nature Conservancy, and the Champaign County Audubon Society. We thank the staff at the Forbes Biological Field Station, D. J. Soucek, and J. M. Levengood for their assistance with the project; M. J. Wetzel and R. E. Dewalt for aid in identification of invertebrates; J. Dassow, B. J. O'Neal, A. Bartlett, and B. T. Kapusta for their assistance in the field and lab; and the staff at the Illinois River National Wildlife and Fish Refuge and Rice Lake State Fish and Wildlife Area. Comments on earlier drafts by G. O. Batzli and three anonymous reviewers greatly improved this paper.

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The Wilson Journal of Ornithology 118(2):164–172, 2006

COMPOSITION AND TIMING OF POSTBREEDING MULTISPECIES FEEDING FLOCKS OF BOREAL FOREST PASSERINES IN WESTERN CANADA

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ABSTRACT.—The aggregation of nonbreeding insectivorous songbirds into multispecies feeding flocks during migration and on their wintering grounds is a well-known and important aspect of their ecology. The establishment of multispecies feeding flocks on the temperate breeding grounds of North American Neotropical migrants, however, remains poorly known or understood. To address this gap, we investigated the composition and timing of flocking behavior among several species occurring in the southern boreal mixed-wood forest of western Canada. Of 67 species observed in 216 flocks, the most abundant were Tennessee Warbler (*Vermivora peregrina*) and several resident species: Black-capped Chickadee (*Poecile atricapillus*), Red-breasted Nuthatch (*Sitta canadensis*), and Boreal Chickadee (*Poecile hudsonica*). Consistent with previous work on Eurasian boreal species, residents appeared to play a pivotal role in flock occurrence and cohesion. Flocking tended to begin in late June, and flock sizes increased throughout the summer. This suggests that unsuccessful breeders, early breeders, and early migrants are the first to join flocks, whereas later-nesting species may delay joining flocks until after their young fledge. We also investigated the propensity of several species to display flocking behavior in areas with and without a superabundant food source—the spruce budworm (*Choristoneura fumiferana*). These data provided some support for the hypothesis that flocking facilitates foraging, as species tended to flock in areas where food abundance was lower. *Received 24 January 2005, accepted 14 December 2005.*

The aggregation of individual insectivorous songbirds into multispecies feeding flocks is a phenomenon that has been noted for some time (e.g., Newton 1896, Sharpe 1905) and has received considerable attention recently (Hutto 1994, Latta and Wunderle 1996, Mönkkönen et al. 1996). Such flocking behavior is interesting from several perspectives, and a number of hypotheses have been put forth to explain the evolution of such interspecific associations, primarily focusing on the avoidance of predation (Pulliam 1973, Elgar 1989) and the facilitation of food finding (Morse 1970, 1977). The establishment and maintenance of hierarchies within flocks and the role of interspecific competition in structuring these aggregations also are areas of considerable interest (Munn and Terborgh 1979, Powell 1979, Hutto 1994).

To date, research on multispecies feeding flocks involving forest passerines has focused primarily on the wintering grounds, particularly in the Neotropics (reviewed by Mönkkönen et al. 1996; see also Buskirk et al. 1972; Hutto 1987, 1994; Ewert and Askins 1991; Latta and Wunderle 1996). This is in spite of the fact that mixed-species flocks of North American songbirds are conspicuous on their breeding grounds or during the early postbreeding migration period. In the continental United States, Morse (1970) was the first to conduct a quantitative study on ecological aspects of mixed-species foraging flocks of songbirds during late summer through winter, but virtually no studies of foraging flocks have been conducted on North American breeding grounds since then. Research by Mönkkönen et al. (1996) on mixed-species foraging aggregations and heterospecific attraction in boreal bird communities in Finland represents an important advance in the study of flocking behavior among temperate-breeding songbirds. These authors determined that feeding associations occurred during the breeding season and that titmice (*Parus* spp.) seemed to play a focal role in the occurrence of these flocks. They also suggested that flocking might produce variation in species numbers, local abundances, and spatial patterns, both within and between communities in boreal forests. To address the paucity of information on multispecies aggregations of boreal forest songbirds on their breeding grounds in North America, we investigated the composition and timing of flocking behavior among several species.

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Within the boreal forest of North America, the southern boreal mixed-wood ecozone supports one of the most diverse breeding bird assemblages of any forest type in the continent (Robbins et al. 1986, Price et al. 1995). Most of the breeding birds are Neotropical or short-distance migrants. In addition, much of the forest occurring in this region is contiguous primary forest that has not yet been altered by logging (but see Stelfox 1995). This is in contrast to Scandinavian boreal forest, which has less complex avian communities with fewer migrants (see Schmiegelow and Mönkkönen 2002). The first objective of our study was to establish the timing and importance of flocking throughout the breeding and immediate postbreeding periods. To accomplish this, we aimed to document occurrences of flocking in relation to overall breeding phenology of the avian community. Second, we sought to document flock composition and evidence of associations among flock members; specifically, we were interested in identifying species integral to flock formation and whether species associations were random or based on foraging guilds or taxonomic affinities. Our third objective was to determine whether flocking was associated with areas where food resources were superabundant—areas with infestations of spruce budworm (*Choristoneura fumiferana*). If flocking was a response to increased foraging efficiency, we expected that species occurring in areas where food is superabundant might be less likely to participate in foraging flocks.

METHODS

Study area and field observations.—The study was conducted from mid-May to mid-September 1992–1996, in the southern boreal mixed-wood forest of west-central Saskatchewan, Canada, primarily in the vicinity of Prince Albert National Park (53° 35′ N, 106° 00′ W), a 387,500-ha block of contiguous primary forest. The dominant tree species in this region were trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and paper birch (*Betula papyrifera*). The majority of the study area burned in 1919; therefore, it is largely uniform in age structure (Weir and Johnson 1998). Forest west of the park had undergone an outbreak of spruce budworm, providing us with an opportunity to sample similar forest habitats in budworm-infested (hereafter "infested") and uninfested (i.e., no budworm infestation) areas. By 1993, approximately 30,000 ha were infested and classified as moderately to severely defoliated (i.e., >50% defoliation; Saskatchewan Natural Resources Forest and Lands Branch 1993). From mid-May to mid-July in >30 mature forest stands, we opportunistically recorded all feeding flocks encountered. For the purposes of this study, we defined a flock as any assemblage of individuals composed of more than one species clearly moving together. We did not include single family groups; however, we did include amalgamations of single-species flocks composed of more than one family group. After mid-July and until mid-August, when flocks became more common, one observer spent at least 6 hr per day searching for flocks along forest trails and riparian edges. Thereafter, observations were again made opportunistically during the course of other fieldwork.

In total, we observed 215 flocks, distributed relatively equally amongst infested (n = 102) and uninfested sites (n = 113). Upon encountering a flock, we followed it for ~20–30 min while counting or estimating the number of individuals of each species and noting the presence of family groups—as evidenced by begging or feeding of young. Flock height, forest type, and location were also recorded.

As part of another study in the same area, from 31 May to 1 July 1992–1996, we also conducted 395 point counts across spruce- or aspen-dominated mixed-wood stand types (Hobson and Bayne 2000). Points were roughly equally distributed among infested (n = 204) and uninfested (n = 191) forest. Six highly skilled observers with at least 6 years experience conducted 10-min point counts from 04:00 to 08:30 CST, during which observers recorded all birds heard or seen within an unlimited-distance radius. Two visits were made to each station during the survey period, once prior to 15 June, and once after 15 June. Relative abundance estimates were based on the maximum count for a species during these two visits. Because these data were collected prior to the routine use of methods to correct for detectability biases, we do not have detectability functions to correct these data;

therefore, estimates of flocking propensity should be interpreted with caution. However, this dataset allowed us to quantify relative abundances as determined by point counts and contrast them with the relative occurrences of species in mixed-species flocks at the regional scale.

Statistical analyses.—Basic descriptive statistics were used to examine the magnitude and frequency of species' occurrences in flocks; values are reported as means ± 1 SD. To examine the probability of species co-occurring in flocks, we conducted tests of independence using G-tests with Williams' correction for continuity. Using 2 × 2 contingency tables, we contrasted the number of flocks (frequency of occurrence) in which species co-occurred and the number of flocks in which one species occurred but the others did not. We used Fisher's exact test of independence when expected frequencies were ≤ 5 (Zar 1996). To evaluate flocking propensity (the occurrence of a species more or less frequently than expected due to chance) of the most abundant species in both infested and uninfested forests, we used a 2 × 2 Yate's-corrected chi-square test for independence; this test contrasted a given species' abundance in flocks and on point counts with the total abundance of all species in flocks and on point counts.

To compare estimated flock size in infested versus uninfested forests, we used analysis of covariance (ANCOVA) on rank-transformed data and included Julian date as the covariate. Shannon Evenness, species richness, and Simpson's, McIntosh, and Shannon diversity indices were used to evaluate flock composition (Magurran 1988). Flock-size estimates were log-transformed and we used linear regression to analyze change in flock size throughout the season. Finally, temporal patterns of flock composition were depicted graphically and Mann-Whitney U-tests were employed to test for significance of change through time and between infested and uninfested areas. We set statistical significance at $\alpha \leq 0.05$; however, Bonferroni adjustments were used for multiple comparisons, resulting in species co-occurrence being assessed at $\alpha \leq 0.0004$ (0.05/120 pairwise comparisons) and flocking propensity being assessed at $\alpha \leq 0.001$ (0.05/52 tests). Scientific names of all bird species are given in Table 1.

RESULTS

We recorded 5,753 individuals representing 67 species in 216 flocks (Table 1). The mean number of species per flock was 6.6 ± 3.3 and the mean number of individuals per flock was 41.1 ± 60.4. The six species occurring most frequently in flocks included a long-distance migrant (Tennessee Warbler), two short-distance migrants (Yellow-rumped Warbler, Chipping Sparrow), and three resident species (Black-capped Chickadee, Red-breasted Nuthatch, Boreal Chickadee).

We evaluated the probability of the 15 most commonly observed (i.e., number of flock occurrences >30) species co-occurring in flocks. Of the 120 possible pair-wise comparisons, we found only 5 significant (positive or negative) associations. Black-capped Chickadee co-occurred with Bay-breasted Warbler 1.6 times less frequently than expected by chance ($G = 15.03$, $P < 0.001$), and there was also a negative association between Boreal Chickadee and American Redstart (2.6 times; $G = 10.66$, $P < 0.001$). Red-breasted Nuthatch associated positively with Brown Creeper 1.4 times more frequently than expected by chance ($G = 15.44$, $P < 0.001$). Among migrants, American Redstart was positively associated with Red-eyed Vireo 1.9 times more frequently than expected by chance ($G = 18.06$, $P < 0.001$) and with Bay-breasted Warbler 7.8 times less frequently than expected by chance ($G = 12.14$, $P < 0.001$).

In both infested and uninfested stands, we compared the abundances of species in flocks with their relative abundances, as determined by regional point counts (Table 2). This provided us with another measure of flocking tendency and whether it changed with resource availability. Controlling for Julian date, flock size was larger in uninfested sites (61.1 ± 78.0 individuals) than in infested areas (20.1 ± 15.6 individuals; $F_{1,152} = 13.23$, $P < 0.001$). In the infested sites, seven species occurred in flocks more than expected and seven less than expected on the basis of their regional relative abundances; 12 species showed no significant association (Table 2). Of the same 26 species considered above, only 9 occurred more frequently in flocks than expected on the basis of their relative abundances, all but 1 of which (Brown Creeper) showed a similar tendency in uninfested sites (Black-capped Chickadee, Yellow-rumped Warbler, Red-breasted Nuthatch, Boreal Chickadee, Dark-eyed Junco, Yellow Warbler). Nine species avoided flocks in uninfested areas and, of these, five species also avoided flocking in the infested sites. Pine Siskin showed less tendency to flock in the infested than in uninfested sites. Six species showed a significant tendency to either avoid or join flocks in one of the two habitats, with no significant trend in the other habitat (Chipping Sparrow, Bay-breasted Warbler, Magnolia Warbler, Black-and-white Warbler, Solitary Vireo, and Dark-eyed Junco).

Flock size and the number of species in flocks generally increased through the season; however, the trend was only significant for flock size ($F_{1,152} = 40.305$, $P < 0.001$; Fig. 1). For all years combined, we compared flock attributes before and after 29 July—the midpoint of our observation period and the date by which most, if not all, nests were expected to have fledged. The number of individuals detected in flocks after 29 July (61.8 ± 77.8, $n = 79$ flocks) was greater than that detected before (19.4 ± 14.8, $n = 75$ flocks; Mann-Whitney $U = 1{,}221.0$, two-tailed $P < 0.001$). The number of species per flock was similar in the first (6.0 ± 2.7, $n = 111$ flocks) and second periods (7.4 ± 3.8, $n = 103$ flocks; Mann-Whitney $U = 4{,}892.5$, two-tailed $P = 0.067$). We also compared indices of flock diversity by infested versus uninfested areas and time period (before and after 29 July). The McIntosh diversity index (Magurran 1988) was higher in uninfested (McU = 15.5 ± 14.6, $n = 114$) than in the infested sites (McU = 9.1 ± 7.3, $n = 100$; Mann-Whitney $U = 3{,}568.5$, two-tailed $P < 0.001$), but no significant difference was found for Simpson or Shannon diversity measures. Shannon Evenness, however, was greater in the infested ($J' = 0.90 \pm 0.09$) than in uninfested sites ($J' = 0.87 \pm 0.12$; Mann-Whitney $U = 4{,}522.0$, two-tailed $P = 0.021$). The McIntosh index was also higher for flocks observed after 29 July (McU = 15.9 ± 15.2) compared with those observed earlier (McU = 9.3 ± 7.0, $n = 214$; Mann-Whitney $U = 3{,}842.5$, two-tailed $P < 0.001$); again, however, we detected no difference in the other measures of diversity. Shannon Evenness was greater in flocks observed before 29 July ($J' = 0.90 \pm 0.09$) compared with those observed later ($J' = 0.87 \pm 0.12$; Mann-Whitney $U = 4{,}244.0$, two-tailed $P = 0.003$).

DISCUSSION

The tendency for species to flock in our study area was widespread among migrants and residents. Tennessee Warbler was one of the migrants most frequently observed flocking, a phenomenon that may be related to its relatively earlier breeding and dispersal in the boreal forest, as well as to its high abundance (Rimmer and McFarland 1998). This species is one of the earliest fall migrants to be recorded at Delta Marsh Bird Observatory (DMBO), a constant-effort mist-netting station just south of our study area (DMBO unpubl. data). Among residents, Black-capped Chickadee, Red-breasted Nuthatch, and Boreal Chickadee were among the most frequently observed flocking species. Similarly, other studies in temperate North America and Europe have revealed that parids and nuthatches occur frequently in multispecies foraging flocks; parids, in particular, have been classified as nuclear species in these aggregations (Morse 1970, Berner and Grubb 1985, Mönkkönen et al. 1996). In our study area, resident boreal species typically breed earlier than migrants and are observed moving in family groups during June when most migrants are still incubating. This phenology may predispose them to serving as catalysts for flocking, similar to their roles in forming fall and winter flocks.

Despite many thousands of hours of fieldwork in the southern boreal mixed-woods from May through September, we observed no mixed-species foraging aggregations until late June. Thereafter, the probability of encountering flocks increased as birds dispersed beyond their territory boundaries. Additionally, flocks tended to be larger later in the season; thus, even though flocks of resident species would move through the territories of migrant species, the migrants apparently did not temporarily join the residents as they passed through (Mönkkönen et al. 1996). Rather, failed breeders or birds in dispersing family groups likely constituted the earliest migrants joining flocks.

TABLE 1. Summary of flocking data for avian species recorded in the southern boreal mixed-wood forest of Saskatchewan, Canada, 1992–1996.

Species	No. individuals (%)	No. flocks in which present (%)	Mean no. per flock (SD)
Tennessee Warbler (*Vermivora peregrina*)	952 (16.55)	146 (67.59)	6.5 (9.1)
Black-capped Chickadee (*Poecile atricapillus*)	854 (14.84)	142 (65.74)	6.0 (7.8)
Yellow-rumped Warbler (*Dendroica coronata*)	635 (11.04)	132 (61.11)	4.8 (6.3)
Red-breasted Nuthatch (*Sitta canadensis*)	383 (6.66)	122 (56.48)	3.1 (2.7)
Boreal Chickadee (*Poecile hudsonica*)	378 (6.57)	81 (37.50)	4.7 (5.1)
Chipping Sparrow (*Spizella passerina*)	355 (6.17)	89 (41.20)	4.0 (3.0)
American Redstart (*Setophaga ruticilla*)	238 (4.14)	35 (16.20)	6.8 (9.9)
Red-eyed Vireo (*Vireo olivaceus*)	207 (3.60)	78 (36.11)	2.7 (2.2)
Pine Siskin (*Carduelis pinus*)	178 (3.09)	26 (12.04)	6.8 (6.2)
Ruby-crowned Kinglet (*Regulus calendula*)	171 (2.97)	57 (26.39)	3.0 (2.3)
Blackburnian Warbler (*Dendroica fusca*)	161 (2.80)	45 (20.83)	3.6 (2.6)
Bay-breasted Warbler (*Dendroica castanea*)	150 (2.61)	48 (22.22)	3.1 (2.5)
White-throated Sparrow (*Zonotrichia albicollis*)	127 (2.21)	33 (15.28)	3.8 (4.6)
Chestnut-sided Warbler (*Dendroica pensylvanica*)	111 (1.93)	21 (9.72)	5.3 (5.9)
Brown Creeper (*Certhia americana*)	104 (1.81)	47 (21.76)	2.2 (1.2)
Magnolia Warbler (*Dendroica magnolia*)	73 (1.27)	40 (18.52)	1.8 (1.3)
Black-throated Green Warbler (*Dendroica virens*)	55 (0.96)	22 (10.19)	2.5 (1.5)
Black-and-white Warbler (*Mniotilta varia*)	52 (0.90)	16 (7.41)	3.3 (3.5)
Cape May Warbler (*Dendroica tigrina*)	51 (0.89)	26 (12.04)	2.0 (1.2)
Blue-headed Vireo (*Vireo solitarius*)	50 (0.87)	16 (7.41)	3.1 (3.4)
Ovenbird (*Seiurus aurocapilla*)	38 (0.66)	27 (12.50)	1.4 (0.8)
Dark-eyed Junco (*Junco hyemalis*)	36 (0.63)	14 (6.48)	2.6 (2.0)
Cedar Waxwing (*Bombycilla cedrorum*)	32 (0.56)	4 (1.85)	8.0 (8.1)
Yellow Warbler (*Dendroica petechia*)	30 (0.52)	11 (5.09)	2.7 (2.1)
Golden-crowned Kinglet (*Regulus satrapa*)	30 (0.52)	6 (2.78)	5.0 (5.5)
Rose-breasted Grosbeak (*Pheucticus melanocephalus*)	29 (0.50)	9 (4.17)	3.2 (3.0)
Canada Warbler (*Wilsonia canadensis*)	27 (0.47)	15 (6.94)	1.8 (1.1)
American Robin (*Turdus migratorius*)	25 (0.43)	5 (2.31)	5.0 (8.4)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	23 (0.40)	15 (6.94)	1.5 (0.6)
White-winged Crossbill (*Loxia leucoptera*)	17 (0.30)	3 (1.39)	5.7
Swainson's Thrush (*Catharus ustulatus*)	14 (0.24)	6 (2.78)	2.3 (2.0)
Flycatcher spp. (*Empidonax* spp.)	14 (0.24)	6 (2.78)	2.3 (0.4)
Hairy Woodpecker (*Picoides villosus*)	12 (0.21)	11 (5.09)	1.1 (0.3)
Mourning Warbler (*Oporornis philadelphia*)	12 (0.21)	9 (4.17)	1.3 (0.7)
Philadelphia Vireo (*Vireo philadelphicus*)	11 (0.19)	7 (3.24)	1.6 (0.5)
Palm Warbler (*Dendroica palmarum*)	9 (0.16)	4 (1.85)	2.3 (1.9)
Purple Finch (*Carpodacus purpureus*)	9 (0.16)	3 (1.39)	3.0
Least Flycatcher (*Empidonax minimus*)	8 (0.14)	5 (2.31)	1.6 (0.9)
Northern Flicker (*Colaptes auratus*)	8 (0.14)	5 (2.31)	1.6 (0.9)
Downy Woodpecker (*Picoides pubescens*)	7 (0.12)	6 (2.78)	1.2 (0.4)
Gray Jay (*Perisoreus canadensis*)	6 (0.10)	3 (1.39)	2.0
Western Tanager (*Piranga ludoviciana*)	6 (0.10)	3 (1.39)	2.0
Alder Flycatcher (*Empidonax alnorum*)	5 (0.09)	1 (0.46)	5.0
Connecticut Warbler (*Oporornis agilis*)	4 (0.07)	3 (1.39)	1.3
Wilson's Warbler (*Wilsonia pusilla*)	4 (0.07)	3 (1.39)	1.3
Evening Grosbeak (*Coccothraustes vespertinus*)	4 (0.07)	2 (0.93)	2.0
Blue Jay (*Cyanocitta cristata*)	4 (0.07)	1 (0.46)	4.0
Kinglet spp. (*Regulus* spp.)	4 (0.07)	1 (0.46)	4.0
Ruby-throated Hummingbird (*Archilochus colubris*)	4 (0.07)	1 (0.46)	4.0
Song Sparrow (*Melospiza melodia*)	4 (0.07)	1 (0.46)	4.0
Common Yellowthroat (*Geothlypis trichas*)	3 (0.05)	2 (0.93)	1.5
Pileated Woodpecker (*Dryocopus pileatus*)	3 (0.05)	2 (0.93)	1.5
Swamp Sparrow (*Melospiza georgiana*)	3 (0.05)	2 (0.93)	1.5
Warbling Vireo (*Vireo gilvus*)	3 (0.05)	2 (0.93)	1.5
Blackpoll Warbler (*Dendroica striata*)	2 (0.03)	2 (0.93)	1.0
Northern Waterthrush (*Seiurus noveboracensis*)	2 (0.03)	2 (0.93)	1.0

TABLE 1. Continued.

Species	No. individuals (%)	No. flocks in which present (%)	Mean no. per flock (SD)
Thrush spp. (*Catharus* spp.)	2 (0.03)	2 (0.93)	1.0
Traill's Flycatcher (*Empidonax traillii*)	2 (0.03)	2 (0.93)	1.0
American Three-toed Woodpecker (*Picoides dorsalis*)	2 (0.03)	2 (0.93)	1.0
American Goldfinch (*Carduelis tristis*)	2 (0.03)	1 (0.46)	2.0
Winter Wren (*Troglodytes troglodytes*)	2 (0.03)	1 (0.46)	2.0
Common Grackle (*Quiscalus quiscula*)	1 (0.02)	1 (0.46)	1.0
Eastern Phoebe (*Sayornis phoebe*)	1 (0.02)	1 (0.46)	1.0
House Wren (*Troglodytes aedon*)	1 (0.02)	1 (0.46)	1.0
Orange-crowned Warbler (*Vermivora celata*)	1 (0.02)	1 (0.46)	1.0
Olive-sided Flycatcher (*Contopus cooperi*)	1 (0.02)	1 (0.46)	1.0
White-breasted Nuthatch (*Sitta carolinensis*)	1 (0.02)	1 (0.46)	1.0
Total	5,753 (100.00)	216	

Overall, we found relatively few significant (positive or negative) species co-occurrences in flocks. Brown Creeper was positively associated with Red-breasted Nuthatch; this likely reflects common foraging habitats. Similarly, the strong negative association between American Redstart and Bay-breasted Warbler likely reflects the very different habitats that these species prefer (i.e., deciduous understory versus coniferous canopy). Instead of strong tendencies for species to associate with others during flocking, we observed random associations of individuals and species more often.

Our flocking propensity results suggest that some species show stronger tendencies to flock than others. In both infested and uninfested sites, Black-capped and Boreal chickadees, Yellow-rumped Warbler, Red-breasted Nuthatch, and Yellow Warbler consistently showed high tendencies to flock, whereas Red-eyed Vireo, White-throated Sparrow, Ovenbird, Cape May Warbler, and Black-throated Green Warbler consistently showed negative tendencies to flock, based on their abundance. There appear to be no strong underlying patterns other than an increased propensity for residents to flock. The flocking propensity trends we observed could have been biased by the low detectabilities of a few species with high-pitched songs (e.g., Brown Creeper, Black-and-white Warbler, Cape May Warbler, and Bay-breasted Warbler); if that were the case, however, our estimates of flocking propensity should have been greater instead of lower because high-pitched species would likely be more detectable in flock surveys (visual) than during point counts (largely auditory).

The two primary hypotheses explaining the occurrence of mixed-species foraging flocks are (1) the reduction of per capita predation risk and (2) greater facilitation of successful foraging due to decreased need for vigilance or insect flushing (Morse 1977, 1980; Krebs and Davies 1981). At sites in Ohio, Berner and Grubb (1985) sought evidence for each hypothesis by experimentally manipulating food abundance during winter and examining the tendency for resident species to flock. They found less flocking in a food-supplemented site versus a control site and so argued that flocking was related more to foraging than to antipredator strategies *per se.* Although we did not manipulate food abundance on our sites, we were able to examine flock composition in uninfested and infested forests of similar composition. Forests infested with spruce budworm are known to provide a superabundant food source for many forest songbirds, including budworm specialists and non-specialists (Zach and Falls 1975, Morse 1989). Flocks in budworm-infested areas were less diverse (i.e., greater community evenness) than those outside of infested areas, likely because flocks in the infested stands were dominated by budworm specialists, such as Cape May Warbler, Tennessee Warbler, and Bay-breasted Warbler. However, we found no general pattern of a greater propensity to flock in uninfested versus infested areas: nine species showed a greater flocking propensity in

TABLE 2. Avian flocking propensity (FP) in sites with and without spruce budworm infestation. Relative abundance, from point-count data and within flocks, is given for each species. FP denotes trend (+, −; 0 = no trend) in flocking propensity—the occurrence of a species in flocks more or less than expected (based on its relative abundance) due to chance.

	Budworm-infested forest					Uninfested forest				
Species	Point count (n = 204)	Flock (n = 102)	χ^2	P	FP	Point count (n = 191)	Flock (n = 113)	χ^2	P	FP
Tennessee Warbler	2,958	312	0.0	0.86	0	455	630	34.8	<0.001	+
Black-capped Chickadee	64	178	1,037.2	<0.001	+	25	660	576.3	<0.001	+
Yellow-rumped Warbler	1,735	239	11.7	<0.001	+	227	395	51.6	<0.001	+
Red-breasted Nuthatch	644	162	91.5	<0.001	+	115	220	37.4	<0.001	+
Boreal Chickadee	268	179	429.2	<0.001	+	40	199	111.0	<0.001	+
Chipping Sparrow	1,444	182	3.8	0.051	0	257	172	11.0	<0.001	−
American Redstart	12	1	0.5	0.82	0	185	231	7.7	0.006	0
Red-eyed Vireo	626	24	25.4	<0.001	−	423	180	76.7	<0.001	−
Pine Siskin	1,174	23	79.7	<0.001	−	81	155	26.5	<0.001	+
Ruby-crowned Kinglet	557	50	1.2	0.27	0	113	121	0.9	0.36	0
Blackburnian Warbler	190	19	0.0	0.88	0	64	146	35.5	<0.001	+
Bay-breasted Warbler	1,186	110	1.8	0.18	0	98	40	19.8	<0.001	−
White-throated Sparrow	668	29	23.0	<0.001	−	290	98	76.7	<0.001	−
Chestnut-sided Warbler	32	0	2.4	0.12	0	85	109	4.2	0.039	0
Brown Creeper	325	80	44.2	<0.001	+	91	24	33.4	<0.001	−
Magnolia Warbler	472	28	8.8	0.003	0	107	45	18.8	<0.001	−
Black-throated Green Warbler	272	10	11.3	<0.001	−	108	45	21.0	<0.001	−
Black-and-white Warbler	6	2	0.8	0.38	0	17	50	17.2	<0.001	+
Cape May Warbler	1,098	35	53.9	<0.001	−	59	16	20.8	<0.001	−
Blue-headed Vireo	290	8	15.7	<0.001	−	50	42	0.2	0.67	0
Ovenbird	2,010	8	194.2	<0.001	−	945	29	725.0	<0.001	−
Dark-eyed Junco	36	26	69.4	<0.001	+	0	10	8.7	0.003	0
Yellow Warbler	0	7	55.4	<0.001	+	0	23	22.4	<0.001	+
Canada Warbler	2	2	3.6	0.059	0	26	25	0.0	0.95	0
Yellow-bellied Sapsucker	112	16	0.9	0.35	0	37	7	17.3	<0.001	0
Hairy Woodpecker	44	4	0.0	0.95	0	19	8	3.1	0.078	0
Total	16,225	1,734				3,917	3,680			

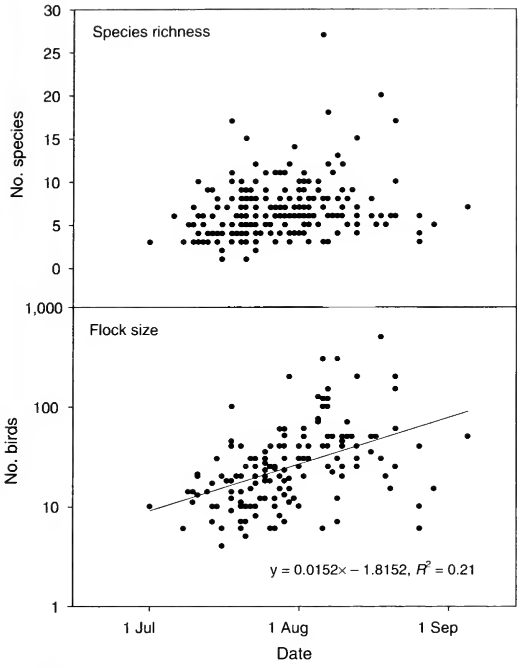

FIG. 1. Temporal patterns in avian flocking, by species richness and flock size, for all species observed in the southern boreal mixed-wood forest of Saskatchewan, Canada, 1992–1996.

uninfested sites and seven had a higher propensity in the infested sites. Flock size, however, tended to be much larger in uninfested sites than in the infested sites. While our results are not entirely unequivocal, they are congruent with the findings of Berner and Grubb (1985) in linking flocking propensity to relative food availability.

Combined, the few trends in species co-occurrences, the inconsistent trends in flocking propensity for most species examined, and the contrasting diversity measures between infested and uninfested sites suggest that flocks are largely representative of local avian communities. Other than resident species, flock structure appears little affected by species' migratory patterns or foraging and nesting guilds. This suggests that the advantages of flocking extend to most species, despite different life-history strategies.

Although we found little structure in patterns of flocking on the breeding grounds, it is well established that flocking does occur in boreal forest bird communities immediately after the young fledge (i.e., as soon as birds are no longer constrained by nesting). The existence of mixed-species flocks during southbound migration suggests that this behavior continues for migrants, possibly until they reach their wintering grounds (Morse 1970). Whether resident or migrant, species that join flocks may engage in non-flocking behavior only during the relatively short breeding period in their life cycle. Additional studies on the breeding grounds as soon as multispecies feeding flocks begin to form are now needed to investigate how flocking relates to other demands, such as post-fledging parental care and molt.

ACKNOWLEDGMENTS

We thank the numerous field assistants who helped collect field data on mixed-species flocks over the course of our investigations, in particular, E. Cumming, who also provided additional data. Our work was funded by the Canadian Wildlife Service and the Prince Albert Model Forest (Project No. 211). We thank M. Mönkkönen and two anonymous reviewers for constructive comments that improved the manuscript.

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The Wilson Journal of Ornithology 118(2):173–177, 2006

VARIATION IN SIZE AND COMPOSITION OF BUFFLEHEAD (*BUCEPHALA ALBEOLA*) AND BARROW'S GOLDENEYE (*BUCEPHALA ISLANDICA*) EGGS

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ABSTRACT.—We investigated the relationships between egg nutrient constituents and fresh egg mass in Bufflehead (*Bucephala albeola*) and Barrow's Goldeneye (*B. islandica*). We found consistently positive relationships between egg mass and yolk, albumen, lipid, mineral, and water (absolute amounts); however, the proportions of nutrient components to fresh mass were highly variable in the eggs of both species (allometric relationships). In Bufflehead eggs, all components except mineral exhibited negative allometry with fresh egg mass. In Barrow's Goldeneye eggs, only mineral exhibited negative allometry, whereas yolk, lipid, and water all exhibited positive allometry with fresh egg mass. Overall, larger eggs of both species contained greater absolute amounts of nutrients; therefore, larger eggs were of better quality than smaller eggs. Nutrient content, however, was more highly correlated with mass in Barrow's Goldeneye eggs than in Bufflehead eggs. We propose that this may be due to the source of egg nutrients: because of their smaller body size, Buffleheads typically rely more on exogenous nutrients than Barrow's Goldeneyes. *Received 5 January 2005, accepted 16 December 2005.*

For many bird species, nutrient content is positively correlated with egg size. Consequently, egg size is often used as an indicator of egg and hatchling quality (Birkhead 1984, Sotherland and Rahn 1987, Pelayo and Clark 2002). There are many potential benefits to laying larger, and presumably better quality, eggs, including increased hatchling size (Alisauskas 1986, Dawson and Clark 1996, Anderson and Alisauskas 2001, Pelayo and Clark 2002), increased growth rate of both embryos and hatchlings (Martin 1987, Badzinski et al. 2002), and higher probability of survival after hatching (Dawson and Clark 1996). Such benefits may lead to selective pressure for females to produce larger eggs with greater protein and lipid stores (Lack 1967). However, the selective pressure to produce larger eggs is constrained by a number of factors, including heredity (Martin 1987), the female's metabolic and physiological capabilities (Rohwer 1988, Thomson et al. 1998), and nutrient availability (Alisauskas and Ankney 1992).

The eggs of species with precocial young, such as waterfowl (Anseriformes), have larger yolks than do those of species with altricial young (Ricklefs 1977). Newly hatched Bufflehead (*Bucephala albeola*) and Barrow's Goldeneye (*B. islandica*) ducklings often struggle to exit their nest cavity, and, once out, they follow the female to the nearest body of water, which may be located immediately below the nest or up to 2 km away (Savard et al. 1991, Gauthier 1993, Eadie et al. 2000). Ducklings must rely on stored yolk reserves until they reach the water and begin to feed (Birkhead 1985). Barrow's Goldeneye and Bufflehead ducklings can experience high mortality rates in the 1st week after hatch due to their inexperience in foraging (Savard et al. 1991). Thus, ducklings with large yolk reserves likely survive for longer periods with little or no food than do those with relatively small yolk reserves.

In some species, nutrient content does not depend on egg size, and the benefits of laying larger eggs may not exist. In the European Starling (*Sturnus vulgaris*), for example, larger eggs contained proportionately less yolk and lipid than smaller eggs (Ricklefs 1984), suggesting that in some species, the chicks that hatch from larger eggs may not experi-

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ence the advantages of proportionately larger yolk reserves.

The primary objective of this study was to determine the relationship between size and nutrient composition in the eggs of Bufflehead and Barrow's Goldeneye breeding in British Columbia. The two species nest sympatrically and have a similar diet (Thompson and Ankney 2002), but they exhibit significant differences in body and egg size.

METHODS

Study area.—The study area included approximately 250 km^2 of the Cariboo Parklands in central British Columbia, Canada (52° 07′ N, 122° 27′ W, approximate center point). Montane and boreal wetlands used by breeding Bufflehead and Barrow's Goldeneye were typically too alkaline and/or too shallow to support fish, and had well developed and diverse aquatic invertebrate communities (for a more detailed description of the study area, see Thompson 1996).

Egg collection and preparation.—Bufflehead (n = 21) and Barrow's Goldeneye (n = 40) clutches were collected in 1993 and 1994 in conjunction with a broader study investigating nutritional strategies for reproduction in these species (Thompson 1996). Digital calipers were used to measure egg length and width (breadth) to the nearest 0.1 mm, and a Mettler balance was used to weigh fresh eggs to the nearest 0.1 g. Eggs were then boiled and frozen, pending analysis. Later, the boiled eggs were thawed and separated into their component parts: yolk, albumen (including egg membranes), and shell. Egg components were dried to a constant mass at 80° C and measured to the nearest 0.01 g. Because egg lipid is confined to the yolk, the dried yolk was washed with petroleum ether in a modified Soxhlet apparatus to extract the lipid component (Dobush et al. 1985).

Statistical analyses.—High rates of intraspecific brood parasitism, particularly for Barrow's Goldeneye, precluded reliable discrimination between eggs of the host and parasite; therefore, within-clutch analyses of variation in egg size and composition were not conducted. For each variable, we inspected a scatter plot to identify eggs that were significantly larger or smaller than average (outliers). Using Principle Component Analyses (PCA), outliers were identified as points on the scatter plot that lay distinctly apart from all others (McGarigal et al. 2000). Outliers exert undue pull on the direction of the component axes, strongly affecting the ecological efficacy of the ordination (McGarigal et al. 2000). A few eggs that deviated noticeably from the norm were removed from the data set. Final sample sizes for Bufflehead and Barrow's Goldeneye (after eliminating outliers) were 123 and 226 eggs, respectively.

Preliminary analysis indicated that the residuals were normally distributed and the data did not exhibit any nonlinear trends. We used linear regression to determine the relationship between absolute amounts of individual egg components (dependent variables: dry yolk, dry albumen, lipid, mineral, and water) and fresh egg mass (independent variable). We examined proportional nutrient content by $\log_{10} - \log_{10}$ (hereafter log-log) regressions of egg components versus fresh egg mass (Alisauskas 1986). A regression slope of unity (b = 1.0) signifies that a component makes up a constant fraction of the total egg mass. Slopes significantly <1 or >1 imply that components make up a decreasing or increasing fraction of the total egg as egg mass increases. For each species, we tested both absolute and proportional variation in egg composition. We used analysis of covariance (ANCOVA) to test whether there was differential partitioning of egg nutrients between the two species. Means and slopes are reported ± SE, and significance was set at $P = 0.05$. All analyses were conducted using MINITAB (Minitab, Inc. 2003).

RESULTS

Dimensions and composition of Bufflehead and Barrow's Goldeneye eggs are presented in Table 1. Fresh mass of Bufflehead eggs consisted of 42% wet yolk, 40% wet albumen, and 9% mineral. Overall, water composed approximately 52% of fresh egg mass. Similarly, the composition of Barrow's Goldeneye eggs averaged 40% wet yolk, 45% wet albumen, and 9% mineral. Water composed approximately 57% of fresh egg mass.

There was a consistently positive relationship between fresh egg mass and absolute amounts of dry yolk, dry albumen, lipid, mineral, and water in the eggs of both species (Table 2). In Bufflehead eggs, all components

TABLE 1. Dimensions (mm) and composition (g) of Bufflehead (n = 123) and Barrow's Goldeneye (n = 226) eggs collected in central British Columbia, 1993–1994.

	Bufflehead		Barrow's Goldeneye	
Variable	Mean ± SE	CV[a] (%)	Mean ± SE	CV[a] (%)
Length	50.20 ± 0.15	3.33	61.69 ± 0.13	3.06
Breadth	36.22 ± 0.07	2.13	43.76 ± 0.06	2.10
Fresh egg mass	36.68 ± 0.19	5.89	66.41 ± 0.22	5.04
Mineral	3.36 ± 0.03	9.82	6.24 ± 0.02	6.09
Wet albumen	14.71 ± 0.22	16.93	30.17 ± 0.23	11.60
Dry albumen	2.66 ± 0.02	9.77	4.94 ± 0.02	7.09
Wet yolk	15.46 ± 0.23	16.24	26.00 ± 0.27	15.65
Dry yolk	7.60 ± 0.06	8.55	13.31 ± 0.06	6.99
Yolk lipid	5.14 ± 0.04	8.95	8.94 ± 0.04	7.27
Yolk protein	2.45 ± 0.02	8.57	4.31 ± 0.02	7.19
Water	19.91 ± 0.14	7.89	37.92 ± 0.21	8.47

[a] Coefficient of variation.

except mineral exhibited negative allometry with egg mass (Table 3). The log-log regression slope for mineral did not differ from unity (b = 0.96 ± 0.11), indicating that mineral mass made up a constant proportion of total egg mass. In Barrow's Goldeneye, yolk, lipid, and water all exhibited positive allometry, whereas mineral exhibited negative allometry and albumen exhibited isometry with egg mass (Table 3). Results of the ANCOVA indicated that the nutrients of Bufflehead and Barrow's Goldeneye eggs are partitioned in different ways; the slopes of the regression lines for each nutrient differed (all $P < 0.001$) between species.

DISCUSSION

The percentages of wet yolk in Bufflehead (42%) and Barrow's Goldeneye eggs (40%) were similar to those reported by Lack (1967) for other waterfowl, such as Common Goldeneye (*Bucephala clangula*; 44%) and Muscovy Duck (*Cairina moschata*; 40%), but were greater than those reported for Greater Snow Goose (*Anser caerulescens atlanticus*; 36%) and Mute Swan (*Cygnus olor*; 34%). In Bufflehead and Barrow's Goldeneye, yolk, albumen, lipid, mineral, and water (absolute amounts) all exhibited a positive relationship with egg size. Log-log regression analysis of component masses versus fresh egg mass indicated interspecific differences. In Bufflehead eggs, all components except mineral exhibited negative allometry with egg mass. In Barrow's Goldeneye eggs, only mineral exhibited negative allometry, whereas yolk, lipid, and water exhibited positive allometry with egg mass. Thus, on average, large Bufflehead eggs do not contain proportionately more nutrients than small eggs, whereas large Barrow's Goldeneye eggs do contain more nutrients than small eggs. The results for Bufflehead are

TABLE 2. Summary of linear regression analyses (egg components versus fresh egg mass; absolute amounts; all $P < 0.001$) for Bufflehead (n = 123) and Barrow's Goldeneye (n = 226) eggs collected in central British Columbia, 1993–1994.

	Bufflehead			Barrow's Goldeneye		
Component	b (SE)[a]	Intercept	r^2	b (SE)[a]	Intercept	r^2
Mineral	0.09 (0.01)	−0.04	0.37	0.06 (0.01)	2.45	0.26
Dry albumen	0.04 (0.01)	0.95	0.15	0.07 (0.00)	−0.01	0.51
Dry yolk	0.15 (0.02)	1.76	0.28	0.23 (0.01)	−1.93	0.69
Yolk lipid	0.11 (0.02)	1.12	0.27	0.16 (0.01)	−1.71	0.67
Yolk protein	0.04 (0.01)	0.83	0.21	0.07 (0.01)	−0.23	0.53
Water	0.32 (0.06)	8.03	0.20	0.67 (0.05)	−6.55	0.49

[a] Slope of regression ± SE.

TABLE 3. Summary of allometric regression analyses (egg components versus fresh egg mass; all $P < 0.001$) for Bufflehead (n = 123) and Barrow's Goldeneye (n = 226) eggs collected in central British Columbia, 1993–1994.

	Bufflehead			Barrow's Goldeneye		
Component	b (SE)[a]	Intercept	r^2	b (SE)[a]	Intercept	r^2
Mineral	0.96 (0.11)	−0.98	0.35	0.60 (0.06)	−0.29	0.26
Dry albumen	0.61 (0.13)	−0.54	0.14	1.00 (0.06)	−1.13	0.52
Dry yolk	0.81 (0.12)	−0.38	0.27	1.12 (0.05)	−0.92	0.68
Yolk lipid	0.80 (0.12)	−0.54	0.25	1.16 (0.05)	−1.16	0.67
Yolk protein	0.68 (0.01)	−0.67	0.20	1.03 (0.05)	−1.25	0.54
Water	0.58 (0.11)	0.39	0.18	1.16 (0.08)	−0.54	0.45

[a] Slope of regression ± SE; a regression slope of unity (b = 1.0) signifies that a component makes up a constant fraction of the total egg mass. Slopes significantly <1 or >1 indicate that components make up a decreasing or increasing fraction of the total egg as egg mass increases.

similar to those of Jager et al. (2000), who found that larger Eurasian Oystercatcher (*Haematopus ostralegus*) eggs contained more lean dry matter and lipid (absolute amounts) than smaller eggs, but the proportion of both constituents decreased with egg size.

In several bird species, hatchlings from large eggs have a higher probability of survival to fledging than do hatchlings from small eggs (Payne 1978). Bufflehead and Barrow's Goldeneye hatchlings were not measured or monitored in this study, therefore it is not known whether large eggs of these species do indeed produce larger ducklings. However, larger Ruddy Duck (*Oxyura jamaicensis*) eggs produced larger, more mature ducklings that were provisioned with greater energy reserves and exhibited greater survival rates than ducklings from smaller eggs (Pelayo and Clark 2002).

Overall, larger eggs in both species contained more nutrients, although nutrient content of Barrow's Goldeneye eggs was more highly correlated with egg mass than it was in Bufflehead eggs (Table 2). This suggests that nutrients in Bufflehead and Barrow's Goldeneye eggs are partitioned differently. A possible mechanism for this difference is the source of egg nutrients: because Buffleheads have a smaller body size, they rely more on exogenous nutrients, whereas the larger Barrow's Goldeneyes can rely more on endogenous nutrients (Thompson 1996, Hobson et al. 2005). This may explain the higher CVs for the constituents of Bufflehead eggs, as they are less able to buffer the effects of variable food supplies by drawing on endogenous reserves.

Our results show that larger eggs of Buffleheads and Barrow's Goldeneyes contain more nutrients than smaller eggs, which may increase the survival of their hatchlings during the 1st crucial week of life. This is especially important given that Buffleheads and Barrow's Goldeneyes nest in boreal and montane regions where food typically is less available than in, for example, the prairie wetlands of North America, used by many temperate nesting ducks (Thompson 1996, Thompson and Ankney 2002). Further studies should be conducted on these species to examine variation in egg composition within and between clutches and to determine whether hatchlings from larger eggs are larger and have lower mortality than those from smaller eggs.

ACKNOWLEDGMENTS

Funding for this project was provided by the National Science and Engineering Research Council of Canada (NSERC) through an operating grant awarded to C. D. Ankney. Additional financial support was provided through a joint Canadian Wildlife Service and NSERC grant awarded by the Pacific Wildlife Research Network Program. We thank the University of Western Ontario and University of Alberta for further financial support for this project as well as use of computer and research labs for data analysis and sample preparation. This research was facilitated by generous cooperation and logistical support provided by M. Clarke, B. Arner, D. Regier, and E. Hennan of Ducks Unlimited Canada, and A. Breault and D. Dockerty of the Canadian Wildlife Service. Permission to work in portions of the study area was kindly granted by the Canadian Department of National Defense (Chilcotin Military Training Area) and B. Durrell of the Wine Glass Ranch. Dedicated field and lab assistance for this project was provided by T. Matthews and S. A. Lee. Finally, we thank G. Robertson and three anonymous reviewers for their constructive feedback on previous versions of this manuscript.

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The Wilson Journal of Ornithology 118(2):178–186, 2006

SITE-SPECIFIC SURVIVAL OF BLACK-HEADED GROSBEAKS AND SPOTTED TOWHEES AT FOUR SITES WITHIN THE SACRAMENTO VALLEY, CALIFORNIA

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ABSTRACT.—We estimated apparent annual survival and recapture probabilities for adult Black-headed Grosbeaks (*Pheucticus melanocephalus*) and Spotted Towhees (*Pipilo maculatus*) at four sites along the Sacramento River, California. To calculate our estimates, we used capture-recapture mist-net data collected over two time periods at four study sites: from 1993 to 1995 at Flynn, Ohm, and Sul Norte, and from 1995 to 2000 at Ohm and Phelan Island. Our primary objective was to determine whether there were site-specific differences in adult survival and recapture probabilities for each species. Such differences are rarely investigated, yet, if present, suggest site-specific differences in habitat quality, with important implications for source/sink dynamics. We found site-specific variation in Black-headed Grosbeak survival within both the 1993–1995 dataset (Flynn = 0.797 ± 0.496, Ohm = 0.158 ± 0.191, Sul Norte = 0.773 ± 0.131) and the 1995–2000 dataset (Ohm = 0.088 ± 0.090, Phelan Island = 0.664 ± 0.111). For Spotted Towhees (1993–1995 data), the most supported model assumed constant survival across sites (0.602 ± 0.240), but there was some support for site variation in survival, as well (Flynn = 0.653 ± 0.365, Ohm = 0.214 ± 0.253, Sul Norte = 0.632 ± 0.258). These results clearly suggest site variation for Black-headed Grosbeaks, and weak evidence of site variation for Spotted Towhees. For both species, the general pattern was low survival at Ohm, suggesting low-quality habitat there and/or reduced site fidelity. The magnitude of site-to-site variation in survival observed in the Black-headed Grosbeak, and suggested for Spotted Towhee, has strong implications for determining source versus sink population status. To determine source versus sink status, we conclude that investigators must not only take into account site variation in reproductive success, but also consider site-specific estimation of adult survival. *Received 28 March 2005, accepted 4 January 2006.*

Measuring adult survival—the probability that an adult will survive from one year to the next—is a critical step toward understanding population dynamics, as low survival rates may be responsible for population declines for some species (Nur and Sydeman 1999). It has been hypothesized that tropical deforestation has led to decreases in over-winter survival (e.g., Askins et al. 1990, Rappole and McDonald 1994), and several recent studies suggest that events at migratory stopover areas also may have significant consequences (e.g., Moore et al. 1995, Yong et al. 1998, Sillett and Holmes 2002). Few researchers, however, have examined the potential role of the breeding grounds in affecting annual survival (Chase et al. 1997, Powell et al. 2000, Sillett and Holmes 2002).

Many factors that are related to a particular species' life-history characteristics operate to influence adult survival at various periods in the annual cycle. Survival of migratory species, for example, may be regulated *primarily* by events during migration or on their wintering grounds in the tropics (e.g., habitat loss). In contrast, all factors influencing the survival of resident species occur on their year-round home ranges. Survival also may be influenced by events during the breeding season in the temperate zone. Reproductive effort can affect survival rates for some species (Nur 1988a, 1988b), and individuals that must make repeated nesting attempts due to high levels of nest depredation may pay a greater cost in terms of survival. For example, female Common House-Martins (*Delichon urbicum*) that double-brooded experienced lower rates of survival than single-brooded females (Bryant 1979). Additionally, environments where the predator community is rich and abundant and habitat cover is poor could negatively influence survival rates.

Despite the widely recognized assumption that survival plays a critical role in regulating populations, few studies of passerines have been designed to specifically look for site- or habitat-specific differences (Peach 1993), though several researchers have examined site fidelity in relation to various indices of site quality (e.g., Bollinger and Gavin 1989, Sedg-

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wick 2004). This is likely because survival is relatively difficult to measure; it requires several years of study, and often-small sample sizes from individual sites prohibit proper analyses. However, site-specific estimates of survival can provide insight into habitat quality, and differences in survival could alert land managers to potential problems.

Here, we present site-specific survival estimates for two species that differ in life history characteristics—the migratory Black-headed Grosbeak (*Pheucticus melanocephalus*) and the resident Spotted Towhee (*Pipilo maculatus*). Our estimates were based on data collected during a multi-site, multi-year, constant-effort mist-netting program (Nur and Geupel 1993) conducted along the Sacramento River. We also investigated differences in recapture probability—the probability that an individual that has survived from year x to year $x + 1$ is also recaptured in year $x + 1$ (Nur and Clobert 1988). As is often the case in attempting to estimate survival, we could not distinguish mortality from permanent dispersal (that is, we measured "local survival"; Lebreton et al. 1992); thus, our estimates are conservative (Lebreton et al. 1992). Site differences in the survival estimates we present may be explained by variation in survival probability from one year to the next, variation in permanent emigration, or both. However, local movements of individuals from year to year (e.g., in some years individuals may have nested closer to, or farther from the array of mist nets) should not have biased our survival estimates; such local dispersal (affecting recapture from one year to the next) is incorporated into our recapture probability calculations (Nur and Clobert 1988).

METHODS

Study sites.—Our four study sites were in the Sacramento Valley, California: Flynn (40° 06′ N, 122° 12′ W), Sul Norte (39° 46′ N, 121° 99′ W), Ohm (40° 09′ N, 122° 12′ W), and Phelan Island (39° 69′ N, 121° 97′ W). Ohm and Flynn were the northern-most sites (3.4 km from each other), Phelan Island was south of these sites by ~50 km, and Sul Norte, located ~100 km south of Ohm and Flynn, was the southern-most site (see map in Gardali et al. in press). Sites ranged in elevation from 39 to 70 m. Dominant trees included Fremont cottonwood (*Populus fremontii*), valley oak (*Quercus lobata*), and willow (*Salix* spp.) with varied understory communities consisting of mugwort (*Artemesia douglasiana*), Santa Barbara sedge (*Carex barbarae*), blue wildrye (*Elymus glaucus*), California blackberry (*Rubus ursinus*), and various exotic, weedy species (e.g., Johnson grass [*Sorghum halepense*], Bermuda grass [*Cynodon dactylon*], Himalayan blackberry [*Rubus discolor*]). Flynn and Sul Norte (in Tehama and Glenn counties, respectively) were riparian remnants of relatively old forests. Ohm (in Tehama County) was also a remnant forest, but differed in that it was grazed by cattle for the duration of the study; thus, the density of the shrub community was diminished in comparison (TG pers. obs.). Ohm also had more black walnut (*Juglans californica*) trees than the other sites (TG pers. obs.). Phelan Island (in Glenn County) was a riparian restoration site planted in 1991 and 1992 (see Alpert et al. 1999 for details). Land use surrounding all sites was primarily agricultural (orchards). Although all sites were broadly similar in plant species composition, landscape context, and climate, there were likely some differences in habitat structure/complexity and flooding frequency.

Field methods.—Black-headed Grosbeaks and Spotted Towhees were sampled through standardized effort mist netting (Monitoring Avian Productivity and Survivorship protocol; DeSante et al. 2000). Sampling occurred at Flynn, Ohm, and Sul Norte during 1993–1995 and at Ohm and Phelan Island during 1995–2000. Ten 12-m, 36-mm-mesh mist nets were operated at each study site for 5 (morning) hr per day for 1 day during each of 10 consecutive 10-day periods (~500 net-hr/site). Starting dates were approximately 1 May and operation continued through the 10–day period ending 8 August. Nets were opened 15 min after sunrise and kept open for 5 hr during each day of net operation. Nets were checked every 20 to 45 min, depending on weather conditions, and were closed when water accumulated on them, or when wind caused net pockets to consistently billow. Because of these standardized protocols, effort (net hr) was similar among sites and years. Captured birds were banded with federal bands, measured, and released immediately.

Statistical analyses.—We used capture/recapture data of adult birds to estimate annual survival, and we used program SURGE 4.3 to calculate recapture probabilities (Lebreton et al. 1992, Cooch et al. 1996). Recapture probabilities of transients can be lower than recapture probabilities of site-faithful individuals in most species (Peach et al. 1991, Chase et al. 1997, Pradel et al. 1997), and such heterogeneity in recapture probabilities violates an assumption of capture-recapture methodology (see Lebreton et al. 1992 for discussion). Various methods have been used to identify site-faithful individuals, such as identifying individuals captured at least twice during any breeding season and/or captured in more than one year (e.g., Chase et al. 1997, Gardali et al. 2000, Nur et al. 2000). In our study, however, we did not recapture enough individuals meeting these criteria to allow such analyses except for (1) Black-headed Grosbeaks at Sul Norte in 1993–1995 and (2) Black-headed Grosbeaks at Phelan Island in 1995–2000. In these two cases, individual Black-headed Grosbeaks captured at least twice during any breeding season and at least 7 days apart, and/or those captured in more than one year were considered site-faithful breeders. We compared survival estimates from this "high site fidelity" subset with those from the full dataset, to determine whether the inclusion of transient Black-headed Grosbeaks biased our survival estimates. All other analyses were based on the full dataset (site-faithful breeders and transients).

For both species and each dataset (i.e., 1993–1995 and 1995–2000), we evaluated four models with time-constant survival (phi) and recapture (p) probabilities to test for potential site-specific variation: (1) constant survival and recapture probability across sites, (2) variable survival but constant recapture probability across sites, (3) variable survival and recapture probability across sites, and (4) constant survival but variable recapture probability across sites. To select the most appropriate model, we employed Akaike's Information Criterion (AIC) and chose the model with the lowest AIC value (Lebreton et al. 1992, Burnham and Anderson 2002). We used differences in AIC between that model and other models to evaluate the evidence in support of particular models. Models with ΔAIC <2 can be said to exhibit moderately strong support relative to the preferred model; those with 2–4 have less support and those with >10 have none (Burnham and Anderson 2002).

TABLE 1. Total numbers of Black-headed Grosbeaks and Spotted Towhees captured, by site and time period, Sacramento Valley, California, 1993–2000.

Years (dataset)	Site	Black-headed Grosbeak (*n*)	Spotted Towhee (*n*)
1993–1995	Flynn	29	30
	Ohm	39	17
	Sul Norte	85	37
1995–2000	Ohm	56	50
	Phelan Island	150	33

We analyzed the data as a partial time series because we did not collect data at all netting sites in all years. Ohm was the only site where mist netting was conducted over the course of the entire study; Flynn and Sul Norte were run from 1993 to 1995 and Phelan Island was operated from 1995 to 2000.

RESULTS

Overall, more Black-headed Grosbeaks were captured than Spotted Towhees (Table 1), but a slightly higher percentage of towhees was recaptured (17.1% versus 12.3%); most of our captures were presumed to be transients. Captures were greatest for both species at Sul Norte (1993 to 1995 data); during 1995 to 2000, we captured more grosbeaks at Phelan Island but more towhees at Ohm (Table 1).

Black-headed Grosbeak.—The model where survival differed across sites while recapture probability was constant performed best (ΔAIC = 0) among the four models (1993 to 1995 dataset; Table 2). Model 3 (both survival and recapture probabilities differed across sites) did not produce maximum-likelihood estimates; boundary estimates were 1.0 for either survival or recapture probability due to the small sample size (Cooch et al. 1996). There was also support for model 4 (constant survival, recapture probability differed across sites; ΔAIC = 0.4; Table 2). The best model from the 1995 to 2000 dataset (model 2) was also the one that supported site-specific variation in survival; there was some support for model 4 as well (ΔAIC = 1.14; Table 2).

TABLE 2. Survival and recapture probabilities for Black-headed Grosbeaks, 1993–1995 (Flynn, Ohm, and Sul Norte) and 1995–2000 (Ohm and Phelan Island), Sacramento Valley, California. Models were (1) constant survival and recapture probability across sites, (2) variable survival but constant recapture probability across sites, (3) variable survival and recapture probability across sites, and (4) constant survival but variable recapture probability across sites. All = all sites combined. AIC_w = AIC weights.

Model	Survival estimate (phi)	SE	Recapture probability estimate (p)	SE	AIC	ΔAIC	AIC_w
1993–1995							
1	All: 0.813	0.327	All: 0.136	0.040	126.63	1.77	0.172
2	Flynn: 0.797	0.496	All: 0.181	0.102	124.86	0	0.417
	Ohm: 0.158	0.191	NA[a]	NA	NA	NA	NA
	Sul Norte: 0.773	0.131	NA	NA	NA	NA	NA
3	Flynn: 1.000	—[b]	Flynn: 0.118	0.090	128.42	3.56	0.070
	Ohm: 0.031	0.053	Ohm: 1.000	—	NA	NA	NA
	Sul Norte: 0.692	0.470	Sul Norte: 0.216	0.134	NA	NA	NA
4	All: 0.762	0.624	Flynn: 0.173	0.280	125.26	0.40	0.341
	NA	NA	Ohm: 0.032	0.077	NA	NA	NA
	NA	NA	Sul Norte: 0.189	0.172	NA	NA	NA
1995–2000							
1	All: 0.642	0.088	All: 0.166	0.046	264.99	13.80	0.001
2	Ohm: 0.088	0.090	All: 0.205	0.054	251.19	0	0.510
	Phelan: 0.664	0.111	NA	NA	NA	NA	NA
3	Ohm: 0.020	0.030	Ohm: 1.000	—	253.06	1.87	0.200
	Phelan: 0.666	0.139	Phelan: 0.204	0.054	NA	NA	NA
4	All: 0.659	0.349	Ohm: 0.017	0.020	252.33	1.14	0.289
	NA	NA	Phelan: 0.208	0.077	NA	NA	NA

[a] NA = not applicable.

[b] Boundary estimates were 1.0 for either survival or recapture probability due to small sample size.

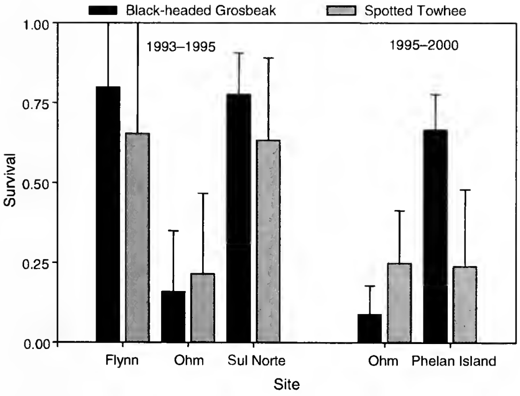

FIG. 1. Site-specific survival estimates for Black-headed Grosbeaks and Spotted Towhees at four sites in the Sacramento Valley, California, over two time periods, 1993–1995 and 1995–2000. For both species, survival estimates from Model 2 (variable survival, but constant recapture probability across sites) are presented (see Tables 2 and 3). Error bars are ± SE.

Overall, we found site-specific variation in survival for Black-headed Grosbeaks within the 1993–1995 dataset (Flynn = 0.797 ± 0.496, Ohm = 0.158 ± 0.191, Sul Norte = 0.773 ± 0.131) and the 1995–2000 dataset (Ohm = 0.088 ± 0.090, Phelan Island = 0.664 ± 0.111; Fig. 1, Table 2).

To investigate whether including transients would bias the full datasets (i.e., those including both transient and site-faithful individuals), we analyzed the subset of data that met our requirements for site-faithful birds. For this, we only estimated constant survival and constant recapture probabilities. At the Sul Norte site (1993–1995 data), the estimate for the site-faithful subset (0.700 ± 0.271) was similar to that of the full dataset (0.773 ± 0.131; Table 2). If transients were biasing results, the survival estimate for the site-faithful subset would have been greater than that for the full dataset, but this was not the case. For Phelan Island (1995–2000), however, the differences in survival estimates (site-faithful

TABLE 3. Survival and recapture probabilities for Spotted Towhees, 1993–1995 (Flynn, Ohm, and Sul Norte) and 1995–2000 (Ohm and Phelan Island), Sacramento Valley, California. Models are (1) constant survival and recapture probability across sites, (2) variable survival but constant recapture probability across sites, (3) variable survival and recapture probability across sites, and (4) constant survival but variable recapture probability across sites. All = all sites combined. AIC_w = AIC weights.

Model	Survival estimate (phi)	SE	Recapture probability estimate (p)	SE	AIC	ΔAIC	AIC_w
1993–1995							
1	All: 0.602	0.240	All: 0.317	0.173	85.06	0	0.512
2	Flynn: 0.653	0.365	All: 0.340	0.180	86.56	1.50	0.242
	Ohm: 0.214	0.253	NA[a]	NA	NA	NA	NA
	Sul Norte: 0.632	0.258	NA	NA	NA	NA	NA
3	Flynn: 0.557	0.501	Flynn: 0.431	0.366	90.18	5.12	0.040
	Ohm: 0.083	0.140	Ohm: 1.000	—[b]	NA	NA	NA
	Sul Norte: 0.752	0.470	Sul Norte: 0.256	0.212	NA	NA	NA
4	All: 0.626	0.532	Flynn: 0.375	0.482	86.87	1.81	0.207
	NA	NA	Ohm: 0.104	0.261	NA	NA	NA
	NA	NA	Sul Norte: 0.324	0.377	NA	NA	NA
1995–2000							
1	All: 0.245	0.111	All: 0.496	0.271	68.98	0	0.508
2	Ohm: 0.248	0.165	All: 0.496	0.272	70.97	1.99	0.188
	Phelan: 0.238	0.241	NA	NA	NA	NA	NA
3	Ohm: 0.296	0.244	Ohm: 0.378	0.373	72.13	3.15	0.105
	Phelan: 0.138	0.170	Phelan: 1.000	—	NA	NA	NA
4	All: 0.237	0.241	Ohm: 0.472	0.453	70.85	1.87	1.990
	NA	NA	Phelan: 0.598	0.596	NA	NA	NA

[a] NA = not applicable.

[b] Boundary estimates were 1.0 for either survival or recapture probability due to small sample size.

subset = 0.739 ± 0.276; full dataset = 0.664 ± 0.111) were consistent with the supposition that transients could have biased our survival estimates, but we could not conclude with confidence that this was the case (Table 2).

Spotted Towhee.—Model 1 (constant survival and recapture probabilities) from the 1993 to 1995 dataset received the most support (Table 3). Models assuming site differences for either survival or recapture probabilities (but not both) also received some support (models 2 and 4). The magnitude of site variation with respect to survival (model 2; Table 3) was large (a difference of 0.41 to 0.43, when comparing Ohm with the other two sites), but the standard errors were large and overlapping (Fig. 1, Table 3).

Model 1 (constant survival and constant recapture probability) was also best (ΔAIC = 0) in the 1995 to 2000 dataset (Table 3). Like those of the earlier dataset (1993–1995), models with site-specific differences in either survival or recapture probabilities (models 2 and 4) could not be ruled out (Table 3). The survival estimates for both Ohm and Phelan Island were very low (model 2; Fig. 1, Table 3). Furthermore, the survival estimates for Ohm were similar in both the 1993–1995 and 1995–2000 time periods, indicating within-site consistency, but Phelan Island also had a low survival rate. Overall, the pattern of site-specific Spotted Towhee survival observed in the 1993 to 1995 data was not manifest in the 1995 to 2000 data.

DISCUSSION

In addition to the site-specific variation we found in survival rates, our survival estimates differed from those published elsewhere. Based on the best-supported models, our survival estimates for Black-headed Grosbeaks at Flynn, Sul Norte, and Phelan Island (0.664 to 0.797) were greater than those calculated (with a modified Cormack-Jolly-Seber method) by DeSante and O'Grady (2000) from 1992–1998 data collected at 51 mist-net stations in northwestern North America (0.573 ± 0.046 SE) and 28 mist-net stations in southwestern North America (0.576 ± 0.051 SE). Survival estimates from the Ohm site (0.088 and 0.158) were considerably lower. Of models assuming constant survival across sites, the best model for all sites combined (model 4; both time periods) also estimated notably higher survival rates than those reported by DeSante and O'Grady (2000). For Spotted Towhees, our 1993 to 1995 survival estimate (0.602) was greater than those found by DeSante and O'Grady (2000) for the northwestern (34 sites) and southwestern (17 sites) regions (0.519 ± 0.047 SE and 0.486 ± 0.043 SE, respectively), whereas our 1995 to 2000 estimate (0.245) was lower.

Site variation in survival was indicated for Black-headed Grosbeaks. There was also some evidence that Spotted Towhee survival varied by site, although the variation around several of these estimates was large and overlapping. For both species, survival estimates at the Ohm site were low; this site differs from the others in that cattle were grazed there during the entire study period. Grazing has the potential to affect habitat quality in several ways, which may influence survival and emigration probabilities (Saab et al. 1995). For example, grazing appeared to have reduced the amount of low shrubby vegetation cover that serves as protection from predators. Heightened predation pressure could negatively affect survival directly via adult mortality, and/or indirectly via nest predation, whereby there is a fitness cost for individuals that renest relatively more than other individuals. Indeed, reproductive effort can affect adult survival rates in some landbird species (Nur 1988a, 1988b; McCleery et al. 1996; Cichon et al. 1998). An additional cause of reduced survival at the grazed site could be related to food resources: fewer insects may have been available because of diminished or modified foraging substrates (but see Haas 1998).

In general, the few past studies conducted to examine over-summer survival (i.e., during the breeding period itself) have revealed relatively high survival rates during this period (Smith 1995, Lahti et al. 1998, Powell et al. 2000, Sillett and Holmes 2002). There is, however, some evidence that subordinate individuals (e.g., young birds) experience higher rates of mortality during this period—primarily due to predation (Geer 1982, Smith 1995, Powell et al. 2000). Additionally, recent evidence suggests that events during one stage in the annual cycle may influence the subsequent stage (Marra et al. 1998, Sillett et al. 2000), and that conditions in one year may affect reproductive performance in a subsequent year (Nur 1988a). Hence, differences in survival caused by differences in conditions on the breeding grounds would not be captured in those studies limited to estimating survival during the summer/breeding season months (Smith 1995, Lahti et al. 1998, Powell et al. 2000, Sillett and Holmes 2002).

Spotted Towhee survival was low at both Ohm and Phelan Island, whereas Black-headed Grosbeak survival was low at Ohm but relatively high at Phelan Island. Although we do not know why towhee survival was low at Phelan Island, this is a restoration site and some vegetation features, or other component of the ecosystem, may have reduced survival.

We could not distinguish true mortality from permanent dispersal. Therefore, observed differences in apparent survival rates may reflect site-specific differences in site fidelity instead of true survival. Such differences also suggest that habitat conditions at Ohm were relatively poor for grosbeaks, and perhaps towhees, because individuals did not remain faithful to that site for multiple years. Several studies have shown that individuals are less likely to return to a territory or site if reproductive performance at that location was poor (e.g., Harvey et al. 1979, Haas 1998, Porneluzi 2003). Interestingly, Haas (1997) found that Brown Thrashers (*Toxostoma rufum*) return significantly more to grazed sites than to ungrazed sites and speculated that thrashers in grazed sites were able to forage more effectively (e.g., preferred substrate) and maintain better body condition.

It is possible that transients may have dominated captures at Ohm, but not at other sites. Perhaps the habitat configuration or net locations at Ohm were more suitable for capturing migrating grosbeaks. However, Spotted Towhees are year-round residents, yet they had low survival estimates at Ohm as well. Also, the Ohm and Flynn sites are only 3.2 km apart, making it difficult to imagine that more migrants would be captured at Ohm. Furthermore, the differences in survival rates between these two sites were so large that it seems unlikely that the cause would have been a preponderance of transients at Ohm (Table 2). Although transient composition may have explained part of the site differences in survival, we believe that the differences are primarily due to true differences in survival. The fact that survival estimates of both species were low at Ohm makes this argument more compelling, and it is likely that both species are being affected by the same mortality factors at that site.

The large differences we found in our survival estimates have strong implications for source-sink dynamics (Pulliam 1988). Whether a site is a source or a sink depends on a combination of adult survival and juvenile recruitment. The low survival rates of Spotted Towhees at Ohm suggest that Ohm is a sink population. Population growth rate (lambda) is equal to the sum of adult survival and net recruitment rate of offspring, which itself is a product of the number of female offspring produced per adult female and the survival of fledged offspring to breeding age (Pulliam 1988, see also Nur and Sydeman 1999). Therefore, a difference in adult survival of 0.40 (such as that found for Spotted Towhees) will lead to a difference in lambda of 0.40 if the other parameter values are the same; thus, if a population is growing at 10% per year at a favorable site (lambda = 1.1), the population would be declining at 30% per year at an unfavorable site, such as Ohm (lambda = 0.70).

For Black-headed Grosbeaks, the differences in apparent survival between Ohm and the other sites were even greater. Adult survival rates of 0.77 to 0.80 at Flynn and Sul Norte (Model 2, 1993 to 1995) may be consistent with those of a source population. At Ohm, with an adult survival rate of 0.19, it would not be possible for a population to yield a lambda of 1.0 or greater (Model 2, 1993 to 1995), even using the most optimistic parameter values for reproductive success and offspring survival. As a result, the Ohm population may be a sink due to low adult survival, irrespective of reproductive success. Alternatively, emigration rates may be high at Ohm because it is a reproductively inferior site resulting in a high turnover of individuals. In this case, survival could be as great at Ohm as at the other sites and Ohm would contribute to the overall metapopulation (Howe et al. 1991).

It is common for researchers modeling site-, treatment-, or habitat-specific lambda to use a single survival estimate in combination with several reproductive estimates (e.g., Donovan et al. 1995, Manolis et al. 2002). The practice has been to use a single survival estimate from one site (not necessarily derived from the study area), regional estimates that combine several sites, or a mean of published estimates. This is understandable because site-specific survival is difficult to estimate, whereas estimating nest survival is relatively easy. Our results, however, emphasize the need to combine site-, treatment-, or habitat-specific estimates of adult survival with comparable estimates of nest survival when modeling population viability.

ACKNOWLEDGMENTS

We are indebted to the many biologists that helped to collect these data, especially A. M. King and S. L. Small. We would like to thank PRBO staff; G. R. Geupel and G. Ballard both contributed to this study in important ways. Funds for this monitoring project came from several sources: The Nature Conservancy, U.S. Fish and Wildlife Service, the David and Lucile Packard Foundation, the William and Flora Hewlett Foundation, the National Fish and Wildlife Foundation, CALFED Bay/Delta Program, the U.S. Bureau of Reclamation, the Natural Resource Conservation Service, and River Partners. We are deeply grateful to all of them. We especially thank our many partners for long-term support: J. Carlon, D. Efseaff, G. Golet, S. Lawson, G. Mensik, S. Phelps, J. Silveira, R. Vega, T. Zimmerman, and D. Zeleke. We thank G. H. Golet, C. A. Haas, and two anonymous reviewers for helpful comments on this manuscript. This is PRBO contribution # 1297.

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The Wilson Journal of Ornithology 118(2):187–193, 2006

PRE-MIGRATORY FATTENING AND MASS GAIN IN FLAMMULATED OWLS IN CENTRAL NEW MEXICO

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ABSTRACT.—Hatching-year (HY) and presumed HY Flammulated Owls (*Otus flammeolus*) were captured during a period of pre-migratory activity in central New Mexico from 2000 to 2003. Mass gains were evident through the pre-migratory period. Fat deposition was an important component of these mass gains; muscle growth appeared to contribute to a lesser degree. Fat scores and pectoral-muscle scores were positively related to body mass and to each other, and, from first to last capture, most recaptured owls showed increases in body mass that were accompanied by fat deposition and growth in pectoral muscles. These data add to a growing body of research indicating that pre-migration increases in fat and muscle mass may be interdependent, but the magnitude of increased muscle mass may be too small to be detected at certain scales. *Received 4 February 2005, accepted 26 November 2005.*

Many migratory birds show substantial gains in body mass prior to migration (King 1972, Bairlein 2002). These gains typically represent some combination of growth in fat, muscle, and organ tissues (King 1972, Lindström and Piersma 1993, Bairlein 2002). Fat is a major component of internal energy reserves and it can be catabolized during migratory flights (King 1972). The amount of fat stored appears to vary in relation to the expected travel distance, opportunities to refuel, and predation risk en route (King 1972, Alerstam and Lindström 1990, Bairlein 2002). Increases in muscle size appear to have a twofold role: to increase the power output from the wings (specifically for pectoral muscles) and to provide a source of amino acids and water as they are catabolized during flight (Marsh 1984, Pennycuick 1998, Lindström et al. 2000, Bairlein 2002). Increases in the size of digestive organs facilitate more rapid uptake of nutrients, aiding in fat storage and the growth of pectoral and other muscles. When not in use, the digestive organs themselves may provide additional nutrient sources as they are catabolized (Karasov and Pinshow 1998, Piersma et al. 1999).

The masses of fat and non-fat tissues often are correlated with overall body mass, but it is not clear that changes in masses of fat and lean tissues are interdependent (Gosler 1991; Selman and Houston 1996; Redfern et al. 2000, 2004). Because changes in mass are related to foraging and behavioral patterns before migration and during migration stopovers, understanding how lean and fat tissues contribute to changes in mass in migratory birds may help to elucidate important aspects of migratory bird ecology (Karasov and Pinshow 1998, Bairlein 2002). The concurrent study of fat deposition, muscle hypertrophy, and mass gain prior to migration has received little attention in field studies, probably because carcass analysis is usually required (e.g., Redfern et al. 2000). Although carcass analysis can provide precise measurements, samples sizes are often small because birds must be killed for analysis. Scoring body composition does not require killing birds and it confers the possibility of adequate sample sizes (Redfern et al. 2004).

Flammulated Owls (*Otus flammeolus*) are small, insectivorous birds that breed in the montane forests of western North America and Mexico (McCallum 1994). The species is believed to winter in southern Mexico and Guatemala; thus, it is considered by most sources to be a Neotropical migrant, undertaking potentially long flights between summering and wintering areas (McCallum 1994). During the falls of 2000–2003, I examined the interrelationships among mass gain, fat deposition, and the size of pectoral muscles in Flammulated Owls captured in central New Mexico. My coworkers and I captured Flammulated Owls from late August, when hatching-year (HY) birds become independent from their parents (Linkhart and Reynolds 1987),

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through October, when birds begin their southward migration. These capture efforts were part of a larger study on the migration ecology of Flammulated Owls (DeLong 2004, DeLong et al. 2005). Based on stable hydrogen isotope analysis of feathers and the stage of the preformative molt, most of the owls had not traveled far from their natal areas (DeLong 2004, DeLong et al. 2005). During latter stages of our field seasons, we captured some migrants that had come from latitudes north of central New Mexico, but they were few in number. Hence, our sampling period was a post-independence/pre-migration period for owls that had summered in central New Mexico. Using this sample, I tested the hypothesis that fat and muscle tissue growth simultaneously contribute to overall mass gain in Flammulated Owls prior to their southward migration.

METHODS

The study site was located near Capilla Peak in the Manzano Mountains of central New Mexico (34° 42′ N, 106° 24′ W). The Manzano Mountains are part of an important migratory corridor for many raptors and songbirds that move through New Mexico during the fall (see DeLong and Hoffman [1999] and DeLong et al. [2005] for additional details). My coworkers and I set up two mist-netting stations, spaced ~200 m apart, one on each side of the north-south trending Capilla Peak ridge. We lured owls to the stations by broadcasting the territorial breeding-season hoots of the male Flammulated Owl from within arrays of 3–6 mist nets (60-mm mesh). From 18 August to 22 October, we opened mist nets 3–7 nights/week, depending on volunteer support and weather. We typically began netting 0–30 min after sunset and continued until 15–30 min before sunrise. We closed the nets when winds exceeded ~24 km/hr or when precipitation began to fall. We checked nets for captured owls every 40–70 min.

We banded owls with federal aluminum leg bands, used an electronic scale to determine their mass to the nearest 0.1 g, and used a standard wing chord ruler to measure their unflattened wing chords to the nearest 1 mm. To determine whether body mass and other parameters of males and females differed, we obtained blood samples or feather shafts from randomly selected HY owls and sent them to Wildlife Genetics, Inc. (Nelson, British Columbia, Canada; www.wildlifegenetics.com) for DNA analysis (CHD gene method; Griffiths et al. 1998).

Whenever possible, we aged owls as either HY or adult. We identified HY owls by the presence of retained juvenal plumage (DeLong 2004) or by uniform fault-barring (Pyle 1997). We identified adult owls by the presence of multiple generations of flight feathers. For the analyses in this paper, I excluded adults because their body mass was significantly greater (HY mean mass = 53.9 g, n = 124; adult mean mass = 59.9 g, n = 13; t = 4.7, $P < 0.001$) and adults were not captured frequently enough to analyze separately. The analyses included both confirmed and presumed HY owls. I presumed that owls of unknown age were HY birds if they were molting their contour feathers, had only a single generation of flight feathers, and weighed less than the mean weight for adults. Most adult Flammulated Owls finish molting their flight feathers by late September (Reynolds and Linkhart 1987), in which case they too would have had a single generation of flight feathers during our study period; thus, it is possible that some adult birds were misidentified as hatching-year birds. For two reasons, however, I believe the number of adults included in the analyses is small. First, most unknown-age owls were captured before October (74% of 128 unknown-age owls) and thus would likely show multiple generations of flight feathers if adult. Second, nearly all of these birds were captured before we were able to use the retained-plumage criterion for identifying hatching-year owls; therefore, these owls were labeled unknown-age only because they did not show multiple generations of flight feathers, not because they lacked retained juvenal plumage. We did not know to look for these feathers in the early years, but learned to do so as the study progressed (DeLong 2004). As the study progressed, it became clear that adult owls were rarely captured at our study site (JPD unpubl. data).

We used a 5-point scoring technique to visually assess the size of pectoral muscles. The pectoral-muscle score was based on thickness (roughly a cross-section), as follows: 1 = muscle very concave with keel of sternum protruding sharply, 2 = muscle roughly triangle-shaped with keel protruding sharply, 3 = rounded muscle with keel still protruding just slightly above the muscle level, 4 = muscle rounded and flush with keel, and 5 = muscle depth exceeds (bulges beyond) the keel. The cross-sectional shape of pectoral muscles is positively correlated with the pectoral mass in small birds (Selman and Houston 1996); therefore, visual assessments of the cross-sectional shape of pectoral muscles should provide a suitable index of pectoral-muscle size. A similar approach has been used effectively in studies of songbirds (Gosler 1991).

We visually assessed furcular fat deposits (i.e., the claviculo-coracoid fat body described by King and Farner 1965) using a 6-point scoring technique similar to that of Helms and Drury (1960). The furcular fat score reflected the depth of fat in the furculum: 0 = no fat, 1 = furculum 1–5% filled with fat, 2 = 5–33% filled, 3 = 34–66% filled, 4 = 67–100% filled, and 5 = fat bulging above furculum. Subcutaneous fat in this region is correlated with overall body fat in small birds—as are fat-scoring procedures, which are based at least partly upon it (Krementz and Pendleton 1990; Rogers 1991; Redfern et al. 2000, 2004). We assigned pectoral-muscle and furcular fat scores to recaptured birds without reference to original capture records.

This study incorporated data from 350 captures, including 9 birds recaptured in the same season; however, sample sizes for some analyses were <350 because we did not record all of the necessary measurements for all birds. I used *t*-tests and Kolmogorov-Smirnov tests to evaluate whether males and females differed in body composition variables. I used linear regression to evaluate the effect of capture date on body mass and fat and pectoral-muscle scores. I used analysis of covariance (ANCOVA) to evaluate the relationship of fat score and body mass, with wing chord length and pectoral-muscle score as covariates. I also evaluated the relationship of pectoral-muscle score and body mass, with wing-chord length and fat score as covariates. These two analyses allowed me to produce mass estimates for each level of each score, having controlled for the effects of the other tissue type and size. Statistical tests were conducted with NCSS 2004 (Hintze 2001) and considered significant if $P < 0.05$.

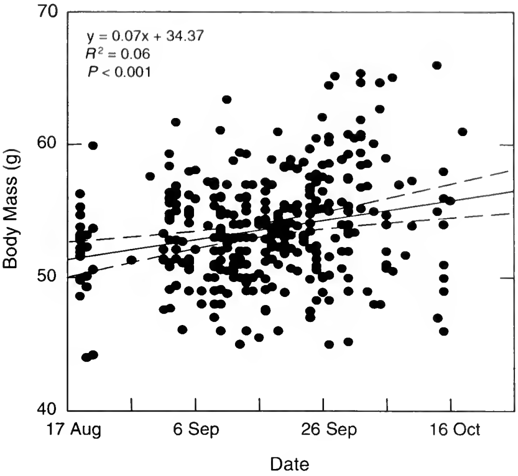

FIG. 1. Body mass (g) of hatching-year Flammulated Owls increased in relation to capture date, showing the gradual gains in body mass through the pre-migration season. The dashed lines represent the 95% confidence interval for the regression line (solid line). Owls were captured during fall at Capilla Peak, New Mexico, 2000–2003.

RESULTS

The number of owls captured varied annually—89 owls were captured in 2000, 157 in 2001, 85 in 2002, and 19 in 2003. Of these 350 owls, our first capture was on 19 August and our last capture was on 18 October, with a median capture date of 17 September.

Of the 88 owls whose sex was determined, 37 were female and 51 were male. Females and males did not differ in body mass ($t = 1.04$, $P = 0.30$, $n = 88$), fat score ($Z = -0.66$, $P = 0.51$, $n = 85$), or pectoral-muscle score ($Z = 0.50$, $P = 0.62$, $n = 88$). Therefore, I combined data for males and females in all further analyses.

Body mass increased through the season in all years, but capture date explained only a small proportion of the variation in body mass ($R^2 = 0.06$, $P < 0.001$, $n = 350$; Fig. 1). Body mass was significantly lower in 2000 than in 2001–2003 ($F_{3,346} = 46.4$, $P < 0.001$, $n = 350$), but there was no body mass × date interaction and no effect on the overall pattern of mass change. Fat scores also increased through the season ($R^2 = 0.19$, $P < 0.001$; Fig. 2). There was a drop in fat scores in mid-

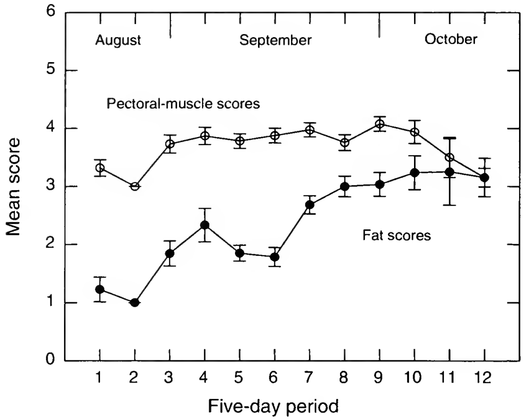

FIG. 2. Mean ± SE fat scores (filled circles) and pectoral-muscle scores (unfilled circles) in relation to capture date for Flammulated Owls captured during fall at Capilla Peak, New Mexico, 2000–2003. Fat scores increased through the season, but pectoral-muscle scores did not. Dates were grouped into 5-day periods from 18 August to 22 October.

TABLE 2. Least-square mean (as derived from ANCOVA, see Table 1) body mass and body mass gain from one score to the next for furcular fat and pectoral-muscle scores of Flammulated Owls at Capilla Peak, New Mexico, 2000–2003.

Scoring regime	*n*	Mass (g)	SE	Gain in mass (g)
Fat				
0	3	51.03	1.97	—[a]
1	61	52.45	0.44	1.4
2	50	53.59	0.48	1.1
3	79	54.63	0.38	1.0
4	61	56.45	0.44	1.8
5	6	58.07	1.39	1.6
Muscle[b]				
2	10	53.29	1.08	—
3	83	53.60	0.37	0.3
4	125	54.73	0.30	1.1
5	42	55.16	0.53	0.4

[a] Gain in mass not calculated for lowest fat and muscle class.
[b] No birds had a pectoral-muscle score of 1.

September (Fig. 2), but fat scores continued to increase after that time. Pectoral-muscle scores did not change through the season ($R^2 = 0.0$, $P = 0.34$; Fig. 2).

ANCOVA revealed that fat scores and pectoral-muscle scores were both related positively to body mass (Table 1). Wing chord length was a strong predictor of body mass, and fat score was a stronger predictor of body mass than pectoral-muscle score (Table 1). Based on least-square means of fat scores (ANCOVA), increments in mass from one fat score to the next ranged from 1.0 to 1.8 g and spanned 7.0 g overall (difference in least-square mean mass of fat scores 0 and 5; Table 2). Mass increments from one pectoral-muscle score to the next ranged from 0.3 to 1.1 g but spanned only 1.9 g overall (difference in least-square mean mass of pectoral-muscle scores 2 and 5).

Based on the mean body mass of the first 10% of captured owls and that of the last 10% captured, the overall mass gain from the beginning to the end of the season was 2.5 g, or 4.8% of initial body mass, and the mean fat score increased from 1.5 to 3.2. Using the data in Table 2, I estimated that fat mass increased by 2 g over the sampling period, or approximately 80% of the total mass increase (i.e., body mass of a bird with a fat score of 3.2 [~55 g] − body mass of a bird with a fat score of 1.5 [~53 g] = a 2-g increase in fat). In contrast, pectoral-muscle scores averaged

TABLE 1. Results of analyses of covariance evaluating the relationships of fat and pectoral-muscle scores versus body mass in Flammulated Owls captured during fall at Capilla Peak, New Mexico, 2000–2003.

Analysis/Factor	df	*F*	*P*
Fat score as main factor			
Fat score	5	9.45	<0.001
Pectoral-muscle score (covariate)	1	6.82	0.009
Wing chord length (covariate)	1	33.29	<0.001
Pectoral-muscle score as main factor			
Pectoral-muscle score	3	2.54	0.057
Fat score (covariate)	1	44.86	<0.001
Wing chord length (covariate)	1	36.78	<0.001

TABLE 3. Nine within-season recaptures of Flammulated Owls indicating changes in mass and body condition indices, Capilla Peak, New Mexico, 2000–2003.

Year	Initial capture date	Days to next capture	Change in mass (g)	Change in fat score	Change in muscle score
2000	9 Sep	19	+5.0	+1	—[a]
2000	10 Sep	5	+2.0	+1	—
2000	9 Sep	18	0.0	—	—
2000	30 Sep	14	+5.0	—	—
2001	2 Sep	21	−2.6	0	0
2001	25 Sep	1	+0.3	0	0
2001	30 Sep	2	+1.0	+1	+1
2002	19 Aug	34	+1.7	+2	+1
2003	5 Sep	9	+2.7	+1	+1

[a] Data not available.

3.5 among both the first 10% and the last 10% of birds captured.

All but two of the owls recaptured later in the same season ($n = 9$) increased in body mass between the initial and second capture, and three of the owls exhibited simultaneous increases in fat and pectoral-muscle scores (Table 3). In addition, scores for fat and pectoral muscle were positively correlated ($r = 0.37$, $P < 0.001$), indicating that owls with high fat scores tended to have high pectoral-muscle scores. Owls showed nearly every combination of fat and pectoral-muscle scores, except for the highest pectoral-muscle score being paired with the lowest fat score, or vice versa.

DISCUSSION

Body mass of Flammulated Owls increased significantly as the migration season approached. This result is consistent with data showing that migratory birds often increase their total body mass prior to migration (Bairlein 2002). Such patterns have been shown for songbirds, shorebirds, and even some diurnal raptors, but little information is available on pre-migration gain in mass among owls (Gessaman 1979, Bairlein 2002). In Colorado, Linkhart and Reynolds (1987) found mass gain in one radio-tracked adult Flammulated Owl during the month of September. In the present study, I confirmed this pattern for a large number of owls, but I also found that capture date explained only a small amount of variation in the mass of captured owls. This latter pattern is not surprising given the expected variation in hatching dates and that owls of different ages likely gain mass at different rates.

I evaluated the relationship of pectoral-muscle size and fat stores to the seasonal increase in body mass in three ways. First, using recapture data, I found that there were concurrent increases in fat scores, muscle scores, and body mass for most individuals. Second, scores of furcular fat and pectoral muscles were closely tied to body mass, but fat scores were better predictors of body mass than pectoral-muscle scores. Third, fat scores increased through the season along with total body mass, but pectoral-muscle scores did not. Taken together, these three results indicate that fat stores are an important component of the overall mass gain in Flammulated Owls prior to migration, but pectoral-muscle size is not as important.

Recently, the question of whether fat stores and muscle tissues develop independently has been raised. For example, Redfern et al. (2000, 2004) found a general interdependence in fat stores and muscle mass for Sedge Warblers (*Acrocephalus schoenobaenus*) and Redwings (*Turdus iliacus*). My data also support the hypothesis that fat and pectoral-muscle scores are interdependent because (1) there were concurrent increases in fat scores, muscle scores, and body mass for most recaptured birds; (2) there was a positive correlation between the variables; and (3) there were no owls having high scores for one parameter without also having high scores for the other.

There appeared to be a non-fat component to the season-long mass gain that was unrelated to pectoral-muscle size. About 20% of the season-long mass gain was not explained by increases in fat mass or pectoral muscle. These increases in mass may have been related to increased sizes of internal organs, which may have been necessary to facilitate the observed accumulation of muscle and fat reserves. Such changes have been observed in other migratory birds as fat reserves were replenished. For example, Karasov and Pinshow (1998) found that internal organ size increased and contributed to gains in body mass among foraging Blackcaps (*Sylvia atricapilla*) captured at a stopover site in Israel during north-bound-migration.

These data add to the growing body of work showing that both fat deposition and muscle growth are associated with migration-related mass gains and that the two processes are somewhat interdependent. The implication of these studies is that birds getting ready to migrate or already migrating may have specific nutrient needs when foraging. This work may help to improve our understanding of foraging ecology and site selection before and during migration—two concerns becoming increasingly important for the conservation of migratory birds.

ACKNOWLEDGMENTS

Primary financial support was provided by the USDA Forest Service (Cibola National Forest and Region 3), the New Mexico Game and Fish Department (Share with Wildlife Program), Public Service Company of New Mexico, and the New Mexico Ornithological Society. Additional funds for the project came from J. and J. Humber. I gratefully thank all of our supporters for their generosity. B. G. deGruyter, H. P. Gross, and J. P. Smith were instrumental in arranging funding and logistical support for this project. I benefited greatly from working with S. L. Stock, who introduced me to, and trained me in, fat- and muscle-scoring techniques for owls. The company and assistance of the Manzano Mountains' field crew and volunteers from both HawkWatch International and Rio Grande Bird Research were greatly appreciated. In particular, W. L. Beard, Z. M. Hurst, W. M. King, and E. A. Snyder made significant contributions to the field effort. I appreciate discussions with J. F. Kelly about migration ecology and analytical techniques. Thanks to J. V. Jewell for support in so many ways. This manuscript benefited from thoughtful reviews by J. F. Kelly, J. P. Smith, and three anonymous reviewers.

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The Wilson Journal of Ornithology 118(2):194–207, 2006

MORPHOLOGICAL VARIATION AND GENETIC STRUCTURE OF GALAPAGOS DOVE (*ZENAIDA GALAPAGOENSIS*) POPULATIONS: ISSUES IN CONSERVATION FOR THE GALAPAGOS BIRD FAUNA

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ABSTRACT.—Island species, particularly endemics, tend to have lower genetic diversity than their continental counterparts. The low genetic variability of endemic species and small populations has a direct impact on the evolutionary potential of those organisms to cope with changing environments. We studied the genetic population structure and morphological differentiation among island populations of the Galapagos Dove (*Zenaida galapagoensis*). Doves were sampled from five islands: Santa Fe, Santiago, Genovesa, Española, and Santa Cruz. Five microsatellite markers were used to determine genetic diversity, population structure, gene flow, and effective population sizes. F_{ST} and R_{ST} values did not differ among populations; in general, populations with greater geographical separation were not more genetically distinct than those closer to one another, and estimated gene flow was high. There were no significant differences in allelic richness and gene diversity among populations. Although there was extensive morphological overlap among individuals from different island populations for both males and females, we found significant differences in overall body size only between populations on Santa Fe and Santa Cruz (males and females) and between Española and Santa Fe (males only). Significant differences in body size between populations undergoing high rates of gene flow indicate that differentiation may be due to either phenotypic plasticity or ecotypic differentiation. Based on the results of previously conducted disease surveys, we discuss the conservation implications for the Galapagos Dove and other endemics of the archipelago; we also discuss the possible effects of wind currents on gene flow. *Received 24 January 2005, accepted 28 November 2005.*

Historically, islands are places where the most dramatic morphological and genetic differentiations have occurred (Grant 1998, 2001). Geographic isolation between populations is expected to promote differentiation of both morphological and genetic characters, due to either drift or different selective regimes (Slatkin 1985, Bohonak 1999). This may reflect population divergence due to insufficient gene flow that would counteract the effects of drift and selection (Slatkin 1985, Hutchison and Templeton 1999, Coleman and Abbott 2003). Isolation leads to the formation of geographical races, which is considered one of the initial stages of speciation (Grant 2001). However, factors independent of geographical isolation (e.g., microclimate, resources, habitat structure) may be acting to create differences between sympatric populations or populations undergoing high gene flow (e.g., Schluter 2001, Ogden and Thorpe 2002). There is also the possibility that morphological differences may be observed—either immediately or within a few generations—at different geographic locations (different populations) without corresponding genetic differentiation (phenotypic plasticity; e.g., James 1983, Losos et al. 1997, Trussell and Etter 2001).

Island species have served as models for studies of evolution due to the discrete nature of island archipelagos and the isolation between different island populations of the same species. Several Galapagos archipelago endemics have very limited inter-island movement, resulting in morphological differences (e.g., Bollmer 2000, Grant 2001). Columbiformes on the other hand are strong fliers able to move long distances (Goodwin 1977, Baptista et al. 1997). Because of the proximity of several islands in the archipelago, we expected high gene flow among populations of the Galapagos Dove (*Zenaida galapagoensis*) and no morphological differentiation.

The Galapagos Dove is an endemic species whose biology and ecology are poorly understood. Our knowledge of this species is restricted to taxonomic relationships (Goodwin 1977, Johnson and Clayton 2000), morphological descriptions (Ridgway 1897, Gifford

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1913, Prestwich 1959), and more recently, to some aspects of its breeding and feeding ecology on Genovesa Island (Grant and Grant 1979). Morphological and ecological studies of bird species in the Galapagos archipelago have been mostly restricted to Darwin's finches (Bowman 1961; Boag 1981, 1983; Grant et al. 1985; Grant 2001), Galapagos mockingbirds (*Nesomimus* spp.; Curry 1988, 1989; Curry and Grant 1989), and the Galapagos Hawk (*Buteo galapagoensis*; de Vries 1973, 1975; Bollmer et al. 2003). Measurements and a general description of Galapagos Doves are provided by Ridgway (1897), Gifford (1913), and Swarth (1931). Gifford (1913) suggested that doves inhabiting the northern-most islands—Wolf (formerly Wenman) and Darwin (formerly Culpepper)—are larger than those located within the main cluster of islands; for this reason, dove populations were classified as two subspecies: *Z. g. exsul* (on Wolf and Darwin) and *Z. g. galapagoensis* (Swarth 1931, Baptista et al. 1997). To assess levels of population structure and morphological variation, our study focused on populations of the southern subspecies (*Z. g. galapagoensis*).

Island species, particularly endemics, tend to have lower genetic diversity than their continental counterparts, especially when such species inhabit small islands (Frankham 1996, 1997). Maintaining genetic diversity and understanding patterns of genetic diversity in natural populations is a central issue in conservation genetics (Frankham 1996, 1997, 1998). Populations are not equivalent in their capacity to adapt to changing environmental conditions, and genetic diversity maximizes the potential evolutionary responses of conserved populations (Petit et al. 1998, Hedrick 2001). Species inhabiting islands are considered behaviorally and physiologically naïve; thus, they might be affected more severely than mainland species by the introduction of predators and diseases (Mack et al. 2000). Demographic and environmental stochasticity can be accentuated in small island populations with little genetic variability, increasing their risk of extinction (Frankham 1996, 1997, 1998).

The introduction of exotic organisms to islands is one of the most important factors in the extinction of endemic species (Wikelski et al. 2004). Because of the negative impact of pathogens on the avian endemics in several other archipelagos, preventing the introduction of avian diseases is a conservation priority in the Galapagos archipelago (Padilla et al. 2004, Wikelski et al. 2004). Some diseases common to Columbiformes, such as *Trichomonas gallinae*, might be transmitted to Galapagos Doves by other Columbiformes, such as the exotic Rock Pigeon (*Columba livia*) and the transient (from South America) Eared Dove (*Z. auriculata*; Harmon et al. 1987, Curry and Stoleson 1988, McQuistion 1991, Mete et al. 2001, Padilla et al. 2004). Padilla et al. (2004) have reported a >85% prevalence of *Haemoproteus* malaria in Galapagos Doves and infections of *Chlamydophila psittaci* in doves inhabiting the island of Española. Buckee et al. (2004) have shown theoretically that host spatial structure directly affects pathogen diversity and strain structure. Thus, it is a conservation priority to understand the movement patterns of those species that could serve as vectors or reservoirs of diseases with interspecific infection potential. We have shown how lice from Galapagos Doves can be transmitted to Galapagos Hawks when they prey on doves; predation may represent a route of transmission for several infectious agents transmitted by lice (Whiteman et al. 2004).

Among the islands sampled in this study, only Santa Cruz was inhabited by humans, and it holds the largest human population of the inhabited islands in the archipelago. Española was the most isolated island, lying at the southeastern extreme of the archipelago. Santa Fe and Genovesa were the smallest islands, and Genovesa was the northern-most island (Fig. 1). The Galapagos islands selected for this study—Santiago, Santa Cruz, Santa Fe, Genovesa, and Española—were chosen to represent the maximum geographic isolation between populations (e.g., Española versus Genovesa) and widest (east-west and north-south) coverage of the archipelago that our budget and logistical restrictions could accommodate. In this study, we (1) used principal components analysis (PCA) to examine morphological variation, (2) used five microsatellite loci to describe the population structure and genetic diversity, and (3) estimated effective population sizes and gene flow of *Z. galapagoensis* on five islands of the Galapagos archipelago: Santiago, Santa Cruz, Santa Fe,

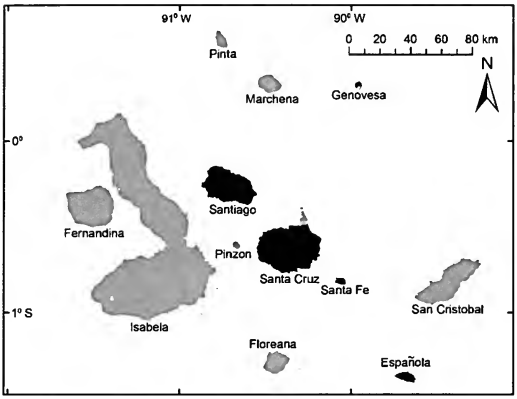

FIG. 1. Map of the Galapagos archipelago, Ecuador, showing the five islands (in dark gray) where Galapagos Doves were sampled in 2002 and 2004. The Galapagos Dove occurs on all the major islands of the archipelago.

Genovesa, and Española. Specifically, we asked (1) are there significant morphological differences among island populations of the Galapagos Dove, (2) are these populations isolated, and (3) is there evidence of low genetic variability in the Galapagos Dove?

METHODS

Field methods.—We conducted our study in the Galapagos archipelago from May through July 2002 and from June through July 2004. Following the guidelines described in Ralph et al. (1996), we captured Galapagos Doves by using hand nets and mist nets. We took blood samples (50 μl each) by venipuncture of the brachial vein from 25 birds each on Santa Cruz, Santa Fe, and Española, and 30 birds each on Santiago and Genovesa islands (Fig. 1). Samples were mixed with 500–700 μl of lysis buffer (100 mM Tris pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire et al. 1988). We also measured 25 birds each from Santa Cruz, Santa Fe, and Española islands and 30 each from Santiago and Genovesa islands (Fig. 1). During the 2002 study season, we sampled doves on San Cristóbal Island, but due to the small sample size (n = 2) they were not included in our analysis. Endemics on San Cristóbal are rare, and the Galapagos Dove seems to be among the rarest.

In order to quantify inter-population differences in morphology, we took the following measurements to the nearest 0.1 mm from the right side of each individual: (1) tarsus length, (2) tail length, (3) length of exposed culmen (from terminus of the feathering to the bill's tip), (4) bill width (calipers were oriented at a 90° angle to the axis of the bill and measurement was taken at the terminus of the feathering), and (5) bill depth (at the terminus of the feathering and again at a 90° angle to the axis of the bill). Using a ruler with a brass perpendicular stop, we also measured wing chord length (unflattened, from carpal joint to the tip of the longest primary) to the nearest 0.5 mm. We used Pesola scales (100 and 300 g) to measure mass to the nearest 0.1 g. Bird measurements were taken by DSA on all the islands but Santa Fe, where J. L. Bollmer conducted the sampling.

Using plumage patterns, we identified birds as adults or juveniles: adults have brighter coloration, and juveniles are much duller in color (Ridgway 1897). Because individual adults of some dove species do not have completely ossified skulls (Pyle 1997), and because the use of cranium calcification (pneumatization) for aging doves is not well developed (Pyle 1997), any captured individual with incomplete calcification and adult coloration was considered an adult. Although it is possible to identify males and females in the field by their plumage coloration and body size (males and females have similar coloration patterns, but males tend to be brighter than females and are larger; Ridgway 1897, Gifford 1913; DSA and PGP unpubl. data), this technique is not always reliable due to individual variation. Therefore, we used a polymerase chain reaction- (PCR) based technique for sexing every individual (Fridolfsson and Ellegren 1999). Birds were released within 40 m of capture location.

Morphology

Statistical analyses.—We used Principal Component Analysis (PCA) to describe morphological variation among islands (SPSS, Inc. 2001). Prior to PCA, variables were checked for outliers (standardizing to zero mean and unit variance); four values with standard deviations ≥2.5 were eliminated. Although all variables (raw data) were normally distributed (Kolmogorov-Smirnov test, $P \geq 0.06$) and have the same scale and dimension (except mass), they were log-transformed in

TABLE 1. Microsatellite primers and number of alleles scored for Galapagos Doves from five islands sampled in 2002 and 2004, Galapagos Islands, Ecuador (n = 134).

Locus	Primer sequence 5′–3′	T_A[a]	No. alleles
WU7a117F	CTC AGT GTA AAT ATG GCA GGG AAT C	54	7
WU7a117R	CAG GTC TTT TTG GTG GAT GTC AC		
WUa38F	GGA GGG CAC CAG AGT TG	55	7
WUa38R	GAT AAG ACC CGA CTT TCA GC		
WUe1F	CAG TGT GGC AGG TAC TTC A	54	3
WUe1R	CTC ATT AGT GGA CCT TGG AC		
WUj22F	CAG GAG CCA TCG TAC ACA T	56	5
WUj22R	TGA ATT ACC CCA TCA ACA AG		
CliμT17	See Traxler et al. 2000	55	11

[a] Annealing temperature (°C).

order to examine proportional contributions of large and small measurements equally. We used PCA on the correlation matrix because one of the variables (mass) did not have the same dimension, and because a PCA on a correlation matrix applied to transformed data is equivalent to a variance-covariance matrix analysis (McGarigal et al. 2000). Furthermore, a PCA from a variance-covariance matrix applied to untransformed (raw) data will give more weight to variables with large variance, which will have a larger influence on the PCA (McGarigal et al. 2000). Because males are larger than females, analyses describing the morphological variation among islands were conducted separately for each sex to prevent the variance due to sexual dimorphism from masking variation among populations. For each PCA, principal component scores were normally distributed (Kolmogorov-Smirnov test, $P \geq 0.74$). Communalities (total variation extracted from each variable) are reported for each PCA. All components with eigenvalues ≥1 were retained for subsequent analyses. Eigenvectors were rotated using varimax rotation and retained when the explained variance was higher than that of unrotated components or when the interpretation of PCs was easier. After conducting a PCA for females, we did not find significant differences between adult and juvenile females ($t_{46} = -0.69$, $P = 0.48$); thus, we retained both groups in the PCA. However, we did find significant differences between adult and juvenile males ($t_{67} = 4.23$, $P < 0.001$) and removed juveniles (15) from the male pool. We excluded female bill depth from the analyses for inter-island comparisons because only one such record was available for Santiago Island. We used *t*-tests and ANOVAs on PC scores for group comparisons and Tukey post-hoc tests any time an ANOVA was significant. In every case, variances of PC scores were homogeneous between and among groups (Levene's test, $P > 0.25$). All *t*-tests were independent and two-tailed.

Genetics

DNA isolation and amplification.—DNA extractions by phenol-chloroform were followed by dialysis in 1× TNE_2 (10 mM Tris-HCl, 10 mM NaCl, 2 mM EDTA) and diluted to a working concentration of 20 ng/μl. Integrity and concentration of each DNA sample was determined by spectrophotometry and electrophoresis in 0.8% agarose gels run in 1× TBE. Individuals were scored at four polymorphic microsatellite loci (Table 1) originally developed for White-winged Doves (*Z. asiatica*; accession numbers for WU7a117, WUe1, WUa38, and WUj22 are AF260574, AF260573, AY428751, and AY428752, respectively) and one locus developed for Rock Pigeon (Traxler et al. 2000). We prepared PCR reactions of 10 μl that included 50 ng of whole genomic DNA, 1 mM dNTP's, 10× reaction buffer, 25 mM $MgCl_2$, 0.5 μg of each primer, 0.1 μl of DMSO, and 0.5 units of *Taq* DNA polymerase (SIGMA). PCR conditions were as follows: initial denaturation at 94° C for 3 min followed by 35 cycles of denaturation at 94° C for 30 sec; annealing from 54 to 56° C (see Table 1) for 1 min and extension at 72 C for 1 min; and a final extension at 72° C for 10 min. PCR products were separated in non-denaturing 7.5% polyacrylamide gels run on BioRad sequencing rigs. Gels were

TABLE 2. Principal component (PC) scores and communalities for seven morphological variables of male ($n = 50$) and female ($n = 52$) Galapagos Doves sampled from five islands in 2002 and 2004, Galapagos Islands, Ecuador. PC scores represent the correlations of each variable with the principal components; communalities represent the sums of squares of correlation coefficients on the first two PCs or the proportion of variance extracted from each variable.

	Males			Females		
Variable	PC1	PC2	Communalities	PC1	PC2	Communalities
Culmen	0.626	−0.212	0.508	0.614	0.515	0.678
Bill width	0.331	0.734	0.762	0.172	0.639	0.918
Bill depth	0.492	0.272	0.550	—[a]	—	—
Tarsus	0.367	0.644	0.888	0.720	0.331	0.629
Tail	0.786	−0.101	0.692	0.421	−0.642	0.820
Wing	0.674	−0.256	0.604	0.790	−0.006	0.739
Weight	0.779	−0.294	0.696	0.606	−0.644	0.787

[a] Not included.

stained with 0.05% ethidium bromide (EtBr) and visualized using a Kodak UV digital imager (KODAK image station 440CF).

Statistical analyses.—We calculated genetic diversity using Nei's unbiased estimator (Nei 1973), which is the probability that two alleles randomly sampled from a population are different. We analyzed allelic richness through rarefaction analysis as implemented by El Mousadik and Petit (1996) and Petit et al. (1998).

F_{ST} estimates outperform R_{ST} counterparts under some circumstances (e.g., when there are allele size constraints in a microsatellite marker, size differences cannot be used to reflect distances among alleles), even under the stepwise mutation model (SMM). Furthermore, R_{ST} can be less accurate at reflecting population differentiation due to its greater associated variance. Even a small number of random mutation events tends to erase part of the memory of the mutation process that is the base of the SMM, which makes R_{ST} estimates superior to F_{ST} only when the mutation process follows the SMM exactly (Gaggiotti et al. 1999, Balloux et al. 2000, Balloux and Lugon-Moulin 2002). Due to the uncertainty of the mutation process of microsatellites (Primmer and Ellegren 1998, Goldstein and Schlötterer 1999), we decided to use *F*-statistics (Weir and Cockerham 1984) for our analysis. For the sake of comparison, we also calculated R_{ST} across samples, and the significance of population differentiation based on F_{ST} was evaluated using a *G*-test and 1,000 randomizations (Goudet et al. 1996). We used pairwise F_{ST} values and geographic distance matrices to test for isolation by distance (Slatkin 1993, Hutchison and Templeton 1999); significance was evaluated with a Mantel test (Mantel 1967) and distance was log-transformed before analysis. Geographical distance was measured as the closest distance between islands.

Data were analyzed for linkage disequilibrium and Hardy-Weinberg equilibrium using F_{IS}, and testing was conducted via *G*-test and randomization procedures (Goudet et al. 1996, Goudet 1999). Bonferroni corrections were applied when appropriate (Rice 1989). Loci proved to be in linkage equilibrium after 200 permutations ($P \geq 0.08$, Bonferroni corrected *P*-value at $\alpha = 0.05$ was 0.005). Samples were under Hardy-Weinberg equilibrium after 500 randomizations, except for one locus/population (WU7a117, $P = 0.002$ for Santiago Island, Bonferroni corrected *P*-value at $\alpha = 0.05$ was 0.002). Therefore, we tested for population differentiation without assuming *H-W* equilibrium. Analyses were conducted using FSTAT (Goudet 2002).

Because gene flow and effective population size estimates based on F_{ST} depend on many unrealistic assumptions (Waples 1998, Whitlock and McCauley 1999), we used a coalescent-based approach to calculate migration rates (Nm) and theta ($\theta = 4Ne\mu$, which is a genetic diversity parameter related to the effective population size [Ne] from which Ne can be estimated) using the program MIGRATE (Beerli and Felsenstein 1999, 2001). Unlike F_{ST}, this program accounts for directional gene flow and for differences in popu-

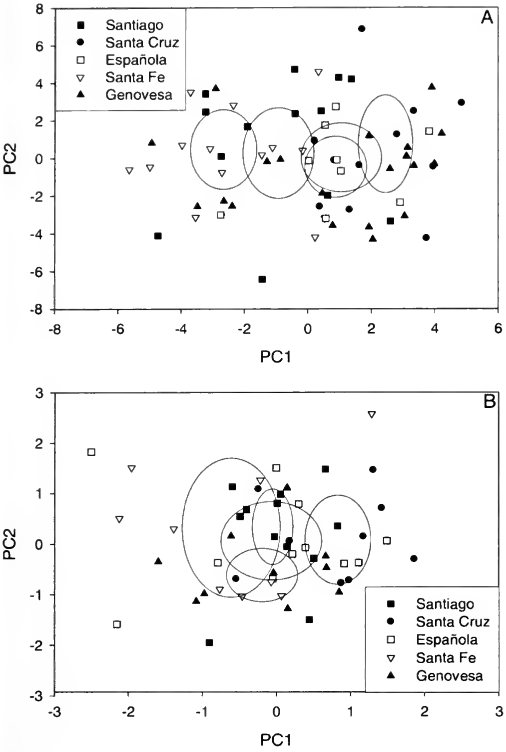

FIG. 2. (A) Morphological ordination space between islands for adult male Galapagos Doves. PC1 is an axis of overall body size and PC2 is a vector reflecting bill size and tarsus length (*n* = 50). Sample sizes per island were as follows: Santiago (18), Santa Cruz (15), Española (11), Santa Fe (15), and Genovesa (20). (B) Morphological ordination space between islands for female Galapagos Doves. PC1 is an axis of overall body size and PC2 is a vector reflecting bill size and tarsus length (*n* = 52). Sample sizes per island were as follows: Santiago (12), Santa Cruz (10), Española (14), Santa Fe (10), and Genovesa (10). Ellipses represent the 95% confidence interval for the different islands.

lation size. We ran the program five times using the estimates of each run as starting parameters for the next one. We assumed equal mutation rates among loci, which is an unrealistic assumption (Goldstein and Schlötterer 1999); however, it provides better estimates of parameters than when using variable mutation rates among loci, which increase the variance (Beerli and Felsenstein 1999). We estimated parameters for the first run, since using an F_{ST} initial estimate produced an attraction to the area of the likelihood surface of the generated F_{ST} values, thus preventing the program from searching efficiently throughout the likelihood surface (P. Beerli pers. comm.). Ten short chains and two long chains were used to calculate parameters. We sampled 500 genealogies for each short chain and 5,000 for each long chain; increments were set to 20 for the short chains and to 100 for the long chains; an initial stabilizing period (burn-in) was set to 10,000 genealogies. We computed multiple estimation of parameters using the two long chains of each run. Because MIGRATE calculates historical migration rates, we used the assignment/exclusion method of Cornuet et al. (1999), implemented in the program GENECLASS (Piry et al. 2004), to estimate current levels of gene flow. This method is appropriate to use when all possible sources of migrants (populations) have not been sampled (Cornuet et al. 1999, Berry et al. 2004). We used the "leave one out" criterion, which removes the individual for which probabilities of assignment/exclusion to a specific population are calculated (Berry et al. 2004). We used the simulation algorithm of Paetkau et al. (2004) to estimate assignment/exclusion probabilities (α = 0.05, 10,000 simulated individuals).

RESULTS

Morphological variation of males among islands.—We retained the first two principal components. PC1, representing an overall size dimension, explained 36% of the variance. PC2, a bill- (width and depth) and tarsus-length component, explained 17% of the variance. The variance extracted from each variable was >50% (Table 2). There were significant differences among islands in the doves' overall body size (PC1, $F_{4,45}$ = 4.99, P = 0.002; Fig. 2a), but not bill size (PC2, $F_{4,45}$ = 1.53, P = 0.21). Based on PC1, Santa Cruz and Española doves were significantly larger than Santa Fe doves (Tukey-test, *HSD* = 1.16, *P* = 0.033 and *HSD* = 1.23, *P* = 0.019, respectively). There is overlap, however, among individuals of these three islands, as well as those from the other islands (Fig. 2a).

Morphological variation of females among islands.—We retained the first two principal components. PC1, which represents an overall size dimension, explained 37% of the variance (Table 2). PC2, a bill- (culmen length and

TABLE 3. Genetic diversity (Nei 1973) and allelic richness for Galapagos Dove, as estimated by rarefaction analysis (Petit et al. 1998) per locus and population. Samples were collected from five islands in 2002 and 2004, Galapagos Islands, Ecuador.

	Genetic diversity				
Locus	SF[b]	E	SC	S	G
Wu7a117	0.75	0.73	0.66	0.69	0.72
Wua38	0.56	0.71	0.52	0.55	0.67
Wue1	0.35	0.42	0.24	0.24	0.31
Wuj22	0.49	0.55	0.62	0.56	0.61
CliμT17	0.79	0.84	0.78	0.84	0.79
Mean ± SD	0.59 ± 0.18	0.65 ± 0.16	0.56 ± 0.20	0.58 ± 0.22	0.62 ± 0.18

[a] R_T = estimated allelic richness for all islands.

[b] SF = Santa Fe, E = Española, SC = Santa Cruz, S = Santiago, G = Genovesa.

width) and tarsus-length component, explained 23% of the variance. The variance extracted from each variable was >62% (Table 2). There were significant differences among islands in overall body size (PC1, $F_{4,47} = 3.14$, $P = 0.023$; Fig. 2b), but not in the second component (PC2, $F_{4,47} = 0.84$, $P = 0.51$). Differences in overall body size were found only among doves from Santa Cruz and Santa Fe, where Santa Cruz females were larger than those from Santa Fe (Tukey-test, $HSD = 1.53$, $P = 0.005$); otherwise there was extensive overlap among individuals from the different islands (Fig. 2b).

Population structure and genetic diversity.—We scored 33 alleles for five polymorphic microsatellite loci from 25 doves on Santa Cruz, Santa Fe, and Española, 30 on Santiago, and 29 on Genovesa. Santa Fe doves had the fewest alleles (23); Española and Santiago had 29 each, Genovesa had 25, and Santa Cruz had 26. The populations with the richest allelic composition (Santiago and Española) had 86% ([29 − 5]/[33 − 5]) of the allelic diversity (excluding the five alleles that were automatically present because there are five loci). Rarefaction analysis showed the same tendency in allelic richness among populations; allelic richness across loci and samples was 27 (Table 3). Genetic diversity was greatest among doves from Española and lowest among those from Santa Cruz; however, there were no significant differences among islands for either allelic richness or genetic diversity (both $P > 0.19$).

Estimates of F_{ST} (0.01, $P > 0.43$) and R_{ST} (0.0057, $P > 0.43$) across samples showed no genetic structure. The 95% bootstrap confidence intervals of the overall F_{ST} estimate were -0.001 and 0.02. No pairwise F_{ST} values were significantly different (all $P \geq 0.025$, Bonferroni corrected P-value at $\alpha = 0.05$ was 0.005; Table 4), and we failed to detect isolation by distance in our data set (Mantel test after 2,000 randomizations, $P > 0.25$).

We estimated high levels of historical gene flow between populations of the Galapagos Dove (Table 5). The highest estimated number of migrants per generation was 71 (Española to Genovesa), which was surprising considering that they are separated by the largest geographic distance (~200 km) compared with distances between the other islands sampled. Genovesa Island had the highest theta value (1.91) and Santa Fe had the lowest (0.18). The high theta for Genovesa is surprising because it is the smallest island of those included in the study; however, Santa Cruz, the largest island, had the second lowest theta value (0.4). If we assume that microsatellite markers have a mutation rate of 10^{-4} events per locus per generation (Goldstein and Schlötterer 1999), and that this mutation rate is the same for each locus, the effective population sizes are as follows: Santa Fe 463; Española 3,600; Santa Cruz 1,000; Santiago 4,600; and Genovesa 4,775. The current high rate of gene flow, as estimated with GENECLASS, suggests that doves are moving among islands. The assignment analysis correctly allocated 27.6% (37) of the individuals ($P \leq 0.009$), but most (34 of 37) had likelihoods lower than the threshold value of being assigned to another population. The difficulties of assigning individuals suggest high current gene flow among populations. Analyses

TABLE 3. Extended.

Allelic richness					
SF	E	SC	S	G	R_T[a]
5	7	6	6.75	4.98	6.11
6	6	5	3.97	4.96	5.46
2	3	2	2.99	2.00	2.56
4	4	4	4.97	4.98	4.61
6	9	9	9.63	7.70	8.25
4.6 ± 1.67	5.8 ± 2.38	5.2 ± 2.58	5.8 ± 2.77	5.0 ± 2.12	5.4 ± 2.08

to detect first generation (F_0) migrants detected 15 migrants ($P \leq 0.05$; Table 6).

DISCUSSION

In this study, we present evidence that populations of Galapagos Doves are morphologically and genetically similar, which must be, in part, the result of high rates of gene flow among islands. However, our results also indicate that there are morphological differences between doves from some island pairs. This might be due to different abiotic and biotic pressures operating on different islands (see below) and to the degree of connectedness (gene flow) between some island pairs (Table 5). For example, Santa Cruz and Santa Fe doves differ in body size (both males and females) and gene flow estimates for these islands are low (see Table 5) even though they are the closest among all the island pairs (17.5 km). Genovesa, the island with the largest effective population size, is the smallest island of those sampled and is also the one receiving the largest number of migrants from the other islands. In addition, it is remarkable that the lowest F_{ST} value and highest numbers of migrants coming to Genovesa are from Española, which is the island most distant from Genovesa (Fig. 1, Tables 4 and 5). Dove populations on both Genovesa and Española, which are small and relatively isolated compared with the central islands (Fig. 1), are the two populations with the greatest genetic diversities, largest estimated population sizes, and highest rates of gene flow (Tables 3 and 5).

Environmental factors such as wind currents might be influencing the travel routes selected by doves from different islands, thus affecting the degree of connectivity among island populations. Several phylogeographic reconstructions of other vertebrate endemics of the archipelago have shown that present and historical wind and ocean currents have had a south-southeast to north-northeast effect on the evolutionary history of organisms (e.g., Caccone et al. 1999, 2002; B. S. Arbogast unpubl. data). However, it is difficult to believe that wind currents are the main reason for movements of Galapagos Doves among islands. Even though there is a high rate of gene flow in a south-to-north direction (e.g., Española to Genovesa [71.4], Española to Santa Cruz [17.85]), gene flow is also high in the

TABLE 4. Estimates of genetic differentiation for Galapagos Doves sampled from five islands in 2002 and 2004, Galapagos Islands, Ecuador. Pairwise F_{ST} values are above, and P-values are below, the dashes (geographic distances in km are given in parentheses). No values were significant (Bonferroni corrected P-value at $\alpha = 0.05$ was 0.002).

Island	Santa Fe	Española	Santa Cruz	Santiago	Genovesa
Santa Fe	—	0.0028	0.0033	−0.0036	0.0090
Española	0.22 (74)	—	0.0264	0.0159	−0.0003
Santa Cruz	0.42 (18)	0.16 (99)	—	−0.0096	0.0372
Santiago	0.10 (76)	0.34 (161)	0.66 (24)	—	0.0160
Genovesa	0.035 (135)	0.20 (204)	0.025 (103)	0.095 (100)	—

TABLE 5. Bi-directional gene flow estimates and theta values (95% CI), estimated with MIGRATE (Beerli and Felsenstein 1999, 2001), for Galapagos Doves from five islands, 2002 and 2004, Galapagos Islands, Ecuador.

Island	Theta ($\theta = 4Ne\mu$)	Nm				
		Santa Fe	Española	Santa Cruz	Santiago	Genovesa
		1 to x[a]	2 to x	3 to x	4 to x	5 to x
1: Santa Fe	0.18 (0.16–0.20)	—	4.64 (4.07–5.26)	4.42 (3.86–5.02)	3.91 (3.31–4.48)	6.75 (6.06–7.50)
2: Española	1.44 (1.31–1.59)	29.24 (27.20–31.38)	—	36.97 (34.67–39.37)	1.32 (0.92–1.82)	14.12 (12.72–15.63)
3: Santa Cruz	0.41 (0.37–0.44)	0.35 (0.19–0.56)	17.85 (16.58–19.18)	—	10.68 (9.70–11.72)	6.39 (5.64–7.20)
4: Santiago	1.84 (1.67–2.03)	6.06 (5.07–7.17)	9.59 (8.34–10.97)	5.66 (4.71–6.73)	—	21.52 (19.61–23.55)
5: Genovesa	1.91 (1.67–2.21)	16.13 (14.11–18.33)	71.47 (67.11–76.00)	13.88 (12.01–15.93)	16.54 (14.49–18.77)	—

[a] The population receiving migrants = x, and the number preceding x is the population from where migrants come. For example, in row 1: Population 2 (Española) provides 4.64 migrants per generation to Population 1 (Santa Fe); Population 3 (Santa Cruz) provides 4.42 migrants; Population 4 (Santiago) provides 3.9 migrants; and Population 5 (Genovesa) provides 6.75 migrants per generation to Population 1.

opposite direction (e.g., Santa Cruz to Española [36.9], Santa Fe to Española [29.2], Genovesa to Santiago [21.5], Genovesa to Española [14.2]; Table 5). Hence, wind currents might not completely account for movements among islands. Perhaps the lack of any clear pattern in dove movement among islands is due to the strong flight capabilities of Columbiformes and the short distances between some islands (<20 km). Doves may simply move between islands to track food resources and suitable environmental conditions. The lack of any pattern in isolation by distance among populations supports the idea that doves can move in any direction.

Low genetic differentiation among dove populations might also be accounted for either by a recent population expansion or by the presence of alleles shared due to common ancestry (e.g., Grant et al. 2005), rather than by frequent dispersal between populations. Rapid population expansion could explain reduced within-population diversity (versus global diversity linked to founder events; Hedrick 2000, McCoy et al. 2003). In our study, estimates of genetic diversity were similar among populations, which would support a gene flow explanation instead of a recent expansion. The possible effect of shared alleles due to common ancestry might be ruled out by the results obtained with GENECLASS, which estimated that current rates of gene flow are high. Moreover, if the Galapagos Dove colonized the archipelago between 2.5 and 3 mya, as proposed by Johnson and Clayton (2000), we should have detected a genetic signature of divergence, given isolation (by distance) between populations.

Morphological variation among islands.—Altitudinal and latitudinal patterns of morphological variation within islands have been confirmed for Darwin's finches, but some patterns are not consistent among islands (Grant et al. 1985). For a given finch species, individuals are larger at higher elevations within any one island, but size variation among island populations is not systematically related to either latitude or longitude. However, this is not the case for other endemic species of the archipelago, such as Galapagos Hawks, where there is a clear north- (smaller size) to-south (larger size) trend in morphological variation (Bollmer et al. 2003). Body size variation in

TABLE 6. Gene flow estimates of first generation migrants (F_0), calculated with GENECLASS (Piry et al. 2004), for Galapagos Doves on five islands, 2002 and 2004, Galapagos Islands, Ecuador. *P*-values are given in parentheses.

	Nm				
Island	Santa Fe	Española	Santa Cruz	Santiago	Geneovesa
	1 to x[a]	2 to x	3 to x	4 to x	5 to x
1: Santa Fe	—	1 (0.039)	1 (0.028)	0	0
2: Española	1 (0.025)	—	1 (0.016)	0	0
3: Santa Cruz	2 (0.027)	1 (0.003)	—	0	1 (0.002)
4: Santiago	1 (0.026)	0	2 (0.026)	—	1 (0.004)
5: Genovesa	0	1 (0.006)	1 (0.035)	1 (0.012)	—

[a] The population receiving migrants = x, and the number preceding x is the population from where migrants come. For example, in row 1: Population 2 (Española) provides 1 migrant per generation to Population 1 (Santa Fe); Population 3 (Santa Cruz) provides 1 migrant; Population 4 (Santiago) provides 0 migrants; and Population 5 (Genovesa) provides 0 migrants per first generation to Population 1.

the Galapagos Dove, however, did not show geographical patterns among the group of islands studied here, most likely because (1) environmental characteristics on the different islands do not vary geographically in a simple manner (Grant et al. 1985), and (2) gene flow for doves among islands is greater than it is for finches or hawks (see below). Moreover, the dove's omnivorous diet (see Grant and Grant 1979) could further impede extensive morphological differentiation between island populations—a situation similar to that of Galapagos mockingbirds (B. S. Arbogast unpubl. data) and Hawaiian thrushes (*Myadestes* spp.; Lovette et al. 2001).

Population structure and conservation.— The lack of population structure and the high levels of gene flow and genetic variation are in stark contrast with results reported for other species in the archipelago, which are characterized by divergence among different island populations and low genetic diversity (e.g., Grant 2001, Bollmer 2000, Bollmer et al. 2003). Allelic richness of the Galapagos Dove for the five microsatellite loci genotyped in this study was similar to the values reported for its continental relatives, White-winged Dove (Tanksley 2000) and Mourning Dove (*Z. macroura*; L. M. Reichart unpubl. data), and in some cases it was greater.

Tanksley (2000) used microsatellite markers and reported no genetic structure in White-winged Doves sampled at a broader geographic scale in North America; mtDNA revealed slight differentiation between populations according to a historical east-west division of its distribution (Pecos River in Texas) that is currently disappearing due to the species' range expansion (Pruett et al. 2000). Pruett et al. (2000) suggested that the White-winged Dove's range expansion is due to urban development, which provides water, food, and nesting sites. Urban development also might be affecting Galapagos Dove populations, at least on the two inhabited islands visited in this study (Santa Cruz and San Cristóbal). Santa Cruz doves had the third lowest number of alleles, second lowest effective population size, and the lowest genetic diversity. On San Cristóbal, extensively surveyed for 3 days, we saw and captured only two doves. Population declines of other endemic bird species on San Cristóbal have been reported (Vargas 1996). The rarity of doves and population declines of other endemic bird species on San Cristóbal seem to be due to the large number of introduced species and to the longer history of human settlement (Vargas 1996). These results provide some support for a negative impact of urban development on Galapagos Doves.

Harmon et al. (1987) reported Galapagos Doves infected with *Trichomonas gallinae* (believed to have been transmitted by Rock Pigeons) on Santa Cruz Island, and Padilla et al. (2004) reported infected Rock Pigeons, but no infected Galapagos Doves. Galapagos Doves on Española were infected with *Chlamydophila psittaci*. The prevalence of *Haemoproteus* spp. in Galapagos Doves was found to be >85% on five islands (Padilla et al. 2004). The presence of infectious diseases and mosquitoes of the genus *Culex* (Wikelski et al. 2004, Whiteman et al. 2005)—the vector of some malaria species—poses serious threats to endemic species. The fact that infectious diseases have resulted in epidemics or epizootics (e.g., *C. psittaci* and *T. gallinae*) in Columbidae and other bird taxa suggests that regular population and disease surveys are needed for Galapagos Doves. High rates of gene flow in Galapagos Doves could contribute to the endangerment of native and endemic species prone to the effects of introduced pathogens that can be transmitted across species (e.g., Galapagos Dove lice being transmitted to Galapagos Hawks during predation; Whiteman et al. 2004). We recommend that the Galapagos Dove be considered a focal species for disease research in the archipelago because it could serve as a reservoir/vector for some infectious diseases (Padilla et al. 2004).

Morphology and dispersal.—That we found morphological differences between some island pairs is not congruent with low genetic differentiation and high rates of gene flow among islands. Lack of concordance between morphology and genetics, however, is not uncommon; through the use of mtDNA markers, it has been reported for other groups, such as reptiles (Schmitt et al. 2000, Brehm et al. 2001), mollusks (Mukaratirwa et al. 1998), insects (Baranyi et al. 1997), and birds (Seutin et al. 1993, 1994; Zink and Dittmann 1993; Freeman-Gallant 1996).

One might expect that morphological differences would have been erased by the connectedness between populations. However, because genes under selective pressure likely control morphological traits, and because F_{ST} assumes neutral markers, selectively neutral markers might not track morphological differences among populations. We do not believe that processes such as genetic drift are important in determining the morphological differences in Galapagos Doves, since they require that gene flow be restricted among populations. Alternatively, morphological characters can be very plastic and might vary within species, depending on the environmental characteristics of an area. Many studies have shown that environmental factors are sufficient to produce morphological changes, either immediately or within a few generations (James 1983, Losos et al. 1997, Trussell and Etter 2001). In other words, environmentally induced differences among populations are independent of genetic differences. Another possibility is that even where dove populations are sympatric and/or affected by high rates of gene flow, there may be an ecotypic-differentiation process driven by divergent selection (Schluter 2001). This has been reported in several studies and for different taxa (Schluter 2001, Ogden and Thorpe 2002). Based on the estimated effective population sizes for the different islands (from ~400 on Santa Fe to ~4,800 on Genovesa), the migration rates (0 to ~70 individuals per generation) represent ~2% of the effective size of the population on the different islands. At this level of migration, the genetic influx might not completely counteract the effects of selection (Conner and Hartl 2004), which could account for the morphological differences observed in our study.

ACKNOWLEDGMENTS

We thank all who provided help during the different stages of the field season, particularly N. K. Whiteman, J. L. Bollmer, G. Jiménez, J. Merkel, J. Rabenold, and N. Gottdenker. We thank the staff of the Charles Darwin Research Station for their invaluable help and logistical support during the course of this study, especially P. Robayo. We also thank N. Freire and J. Miranda who helped with dove sampling at Tortuga Bay, Santa Cruz. Permits for sample collection were provided by Galapagos National Park. We thank B. A. Loiselle, R. E. Ricklefs, B. T. Ryder, A. Cohen, and J. L. Bollmer for helpful comments and suggestions on earlier versions of this manuscript. We thank H. Vargas for sharing his knowledge of Galapagos Doves from islands not visited in this study. We thank P. Beerli who provided guidance on using program MIGRATE. We thank R. L. Curry and two anonymous reviewers for comments that greatly improved the manuscript. Financial support was provided by The International Center for Tropical Ecology, The Saint Louis Zoo, and E. Des Lee Collaborative Vision in Zoological Research.

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The Wilson Journal of Ornithology 118(2):208–217, 2006

BREEDING ECOLOGY OF AMERICAN AND CARIBBEAN COOTS AT SOUTHGATE POND, ST. CROIX: USE OF WOODY VEGETATION

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ABSTRACT.—American (*Fulica americana*) and Caribbean (*F. caribaea*) coots nested colonially at brackish Southgate Pond, St. Croix, United States Virgin Islands (USVI), following a 50-year rainfall event in mid-November 2003. Breeding occurred during three time periods: seven pairs bred from 6 December to 2 January (early), seven from 17 January to 15 February (middle), and eight from 26 April to 19 May (late) (range of clutch initiation dates = 165 days). Hatching success was high (65.3%), but overall reproductive success was low (27%) owing to poor brood survival. Coots built all but 2 of 22 nests at the water line in sturdy crotches of small, live white mangroves (*Laguncularia racemosa*); two late nests were built on remnant stubs of dead white mangroves after water levels had sharply declined. Early pairs nested in manglars (islets of one or more mangroves without solid land) farther away from shore and in deeper water than middle or late pairs (65.6 versus 42.1 and 29.0 cm, respectively). Southgate Pond remains the preferred breeding site for coots on St. Croix and the USVI. Coots have also recently nested on St. Croix at seven semi-permanent or permanent, man-made, freshwater ponds where they have probably been overlooked, as coots respond rapidly to changes in water levels at semi-permanent or permanent wetlands. Predominance of non-assortative pairing at Southgate Pond suggests that American and Caribbean coots are morphs of one species. *Received 7 February 2005, accepted 7 November 2005.*

The Caribbean Coot (*Fulica caribaea*) is not globally threatened (Taylor 1996), but the species is listed as locally endangered in the United States Virgin Islands (USVI; Indigenous and Endangered Species Act of 1990) and is considered threatened throughout the West Indies, especially breeding populations (Raffaele et al. 1973, 1998). Caribbean and American (*F. americana*) coots are two of the rarest bird species that nest in wetlands of the USVI, including St. Croix (Beatty 1930, Raffaele 1989), and their breeding ecology in the Caribbean is poorly known (Taylor 1996, Brisbin et al. 2002). In North America, American Coots are associated with freshwater marshes and low-salinity brackish wetlands (Kantrud 1985).

Following the largest rainfall event in over 50 years, we studied the breeding ecology of Caribbean and American coots at Southgate Pond, the largest seasonal brackish pond on St. Croix. Although degraded by previous coastal development, Southgate Pond is still one of the most productive mangrove wetlands for birds on St. Croix (Scott and Carbonell 1986, Sladen 1992; DBM and CCB unpubl. data). We describe coot breeding adaptations in use of woody vegetation as nest sites (Sugden 1979), and provide information on phenology, clutch size, and breeding success. We also present recent breeding information (since 2002) on coots for seven other sites on St. Croix, formulate management strategies (especially for Southgate Pond), and assess the taxonomic significance of pairing between the two species.

METHODS

During 2003–2004, we studied American and Caribbean coots at Southgate Pond, a 17.9-ha wetland (17° 45′ 29.6″ N, 64° 39′ 45.9″ W) on St. Croix, USVI. We used the criteria of Roberson and Baptista (1988) to distinguish American (types A and B) from Caribbean coots (types C, D, and E) in the field. A small percentage ($\leq$1.4%) of the males with broad, high, and bulbous shields may be white-shielded morphs of American Coots (Roberson and Baptista 1988). Types A and B have a dark chestnut or red-brown corneous callus, whereas types C, D, and E lack a callus. After becoming familiar with vocal dif-

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ferences between the sexes (Gullion 1950), we also identified the genders of some coots at their nests. Males were larger than females and had larger shields and bills, regardless of species, which agrees with expectations based on size and hormonal differences between the sexes (Gullion 1951; Fredrickson 1968, 1970).

We visited Southgate Pond twice a week after the first nest was discovered in early January 2004. Nests were marked with numbered flagging and the location of each nest was recorded with a Global Positioning System (GPS) unit and plotted on a map using ArcView 3.2. We recorded the coot species associated with each nest and coot behavior during each nest visit. Some individuals were not identified to species because of their elusive behavior. Dates of clutch initiation for nests found during laying were calculated by backdating and assuming that one egg was laid per day (Gorenzel et al. 1982, Brisbin et al. 2002). Assuming a 23-day incubation period (Brisbin et al. 2002), initiation dates for nests found after laying were estimated based on hatch dates minus 1 day (the day on which the first egg hatched). For failed nests, we adjusted hatch date for incomplete or under-recorded clutch sizes based on the mean clutch size and backdating from the midpoint between the first and last egg dates. Because our potential renest intervals were long, renests were not assigned to any one pair of coots (based on criteria in Arnold 1993).

We used the method of Mayfield (1975), as modified by Johnson (1979), to calculate hatching success (based on a 23-day incubation period). To determine reproductive success, we followed the fate of individuals and broods until they were fully grown and independent (60–70 days; Taylor 1996). Young coots leave the nest on the day of hatching and broods are difficult to count accurately when young birds hide in emergent vegetation (Gullion 1956); however, emergent vegetation was scarce at Southgate Pond. As young acquired juvenal plumage (~3 weeks old) they left the breeding area for deeper water along the northwestern shore of Southgate Pond, where different broods coalesced into larger flocks and were easier to see and count. All nesting attempts had known outcomes and we calculated reproductive success (number of young fledged/number of eggs laid) by (1) multiplying the number of active nests by mean clutch size to derive an estimate of the total number of eggs laid, and (2) dividing the number of fully grown and independent young (not broods *per se*) by eggs laid. Fledging success (number of young fledged/number of eggs hatched) was determined by dividing reproductive success by hatching success. The number of breeding pairs was based on the number of active nests. Coot nest density at Southgate Pond and the seven man-made freshwater ponds was calculated based on pond area and the number of nests or pairs simultaneously active at each pond. Assessment of intraspecific brood parasitism ("nest-dumping") followed the criteria of Post and Seals (2000).

We recorded the following parameters at each active nest and nest site: nest height from the water line to the top of the nest rim (cm), length and width of outer nest cup (cm), length and width of inner lining (cm), water depth below the nest (cm), above-water height (cm) and greatest breadth (m) of the white mangrove, distance to nearest white mangrove (m), distance to nearest shoreline (m), distance to nearest active nest (m), and distance to nearest active or inactive nest (m). For each pair of coots, four variables (water depth below the nest, distance from the water line to the top of the nest rim, height of white mangrove above water, distance to nearest shoreline) were adjusted to the date of clutch initiation. We also noted whether white mangroves that contained nests were isolated manglars (islets of one or more mangroves without solid land) or formed a line of connected manglars away from the shoreline. We used a bathymetric map of Southgate Pond to adjust distances between nests and the shoreline by taking the mean value of four distance measurements from the −15.25 to 30.5 cm contour (−0.5 to 1 foot) centered on the main breeding area. We then used sine/cosine functions to calculate an angle of 0.026 degrees, which translated to a 1.9-m change in shoreline distance per cm drop (or rise) in water levels. Baseline water level data (in cm) were recorded *in situ* from several 2-m sticks placed in the lowest bed of the flat-bottomed pond. The water level decline was nearly constant throughout the study period (mean of 0.58 cm/day), except for one heavy rainfall event when water levels rose 17 cm from 16 to 18 April. We obtained monthly measurements of salinity at Southgate Pond using a temperature-compensated refractometer (accurate to within ± 1 ppt). From December 2003 through July 2004, salinity increased from 4 to 32 ppt as water levels dropped.

To systematically sample coot breeding habitat, we established a grid of 56 line transects, spaced 8 m apart along north-south cardinal directions from 15 m west of the southwestern shoreline and extending to the eastern point of Southgate Pond just beyond the main coot colony. We randomly selected sample points ($n = 436$) every 8 m along each transect. The last point along each transect was a point in open water beyond the vegetation farthest from shore. Water depth (cm), vegetation present or absent (open water), and species composition (if vegetation present) were sampled at each point. We used a random number generator to assign numbers 1 to 22 (i.e., corresponding to the number of coot nests we found) to sample points of water depth. Water depth at each sampled point that contained vegetation was then adjusted to reflect water depth at the observed or estimated date of clutch initiation for each coot nest represented by each random number (e.g., random number one represents coot nest one, which initiated incubation on 6 December). This procedure removed the effects of declining water levels so that vegetation data would be comparable to nest data.

To assess differences in water depths between vegetation and open water and among species of plants, we used two-tailed t-tests and one-way ANOVA (Zar 1999, StatSoft 2002). Because the sample sizes for five of the eight vegetative species/types recorded were small (total $n = 15$), we did not include them in the ANOVA. We used simple linear regression to assess the relationship between water depth below nests and the date of clutch initiation. We used a Mann-Whitney U-test to assess whether water depths at coot nests differed from random and to examine whether phenological or habitat variables were related to hatching outcome (success/fail). We used nonparametric tests (Mann-Whitney U, Kruskal-Wallis H, and Spearman's rank correlation r_s) when sample sizes were small and data did not otherwise meet assumptions of the normal distribution, including homogeneity of variances and distribution of residuals. For all tests, we used an α value of 0.05. Means are reported ± SD.

RESULTS

We located 22 active coot nests at Southgate Pond during winter and spring of 2003–2004. Dates of clutch initiation ranged from 6 December to 19 May (165 days), with breeding occurring during three periods: early (6 December to 2 January; 27 days), middle (17 January to 15 February; 29 days), and late (26 April to 19 May; 23 days). One nesting attempt during the late period was overlooked (see below). We identified one pair of Caribbean Coots and five Caribbean × American coot pairs (hereafter mixed pairs) during the early period, two pairs of Caribbean Coots and four mixed pairs during the middle period (two male American and two female Caribbean coots were sexed in two of these four mixed pairs), and three pairs of Caribbean Coots and two mixed pairs during the late period (both males were American and both females were Caribbean coots). One of the American Coots of one mixed pair during each of the first two periods was type B (intermediate, *sensu* Roberson and Baptista 1988). The other American Coots appeared to be type A birds. Of the three coots whose mates were not identified, two were Caribbean and one was American.

Clutch size decreased as the nesting season progressed ($r_s = -0.56$, $P = 0.025$) and averaged 6.88 ± 1.41 eggs (range = 5–9, $n = 16$). Seventeen of 22 nests (77%) hatched at least one chick, and only 5 of the 130 eggs (3.8%) that remained unbroken in the nest bowl throughout the normal incubation period failed to hatch. Daily nest survival (s) was 0.982 ± 0.008 SE and hatching success was 65.3% (Mayfield method). Hatching success was not related to clutch initiation dates ($U = 26$, $Z = 1.29$, $P = 0.20$) or any other phenological or habitat variable, although successful nests generally began earlier and had larger clutches, greater water depths, and were farther away from shore than failed nests. Forty-one young became fully grown and independent 60–70 days after hatching. This excludes three young—attended by a pair of Caribbean Coots—that fledged from a ninth nest over-

TABLE 1. Measurements of 14 nest and nest-site parameters for 22 coot nests built in white mangroves at Southgate Pond, St. Croix, U.S. Virgin Islands, during winter and spring of 2003–2004.

Parameter	Mean ± SD	Range
Nest height from water line to top of nest rim (cm)	13.5 ± 6.9	4.8–35.5
Length of outer nest cup (cm)	35.9 ± 8.8	25.4–61.0
Width of outer nest cup (cm)	28.6 ± 4.2	20.3–36.2
Length of inner lining (cm)	19.8 ± 2.2	15.5–25.4
Width of inner lining (cm)	18.0 ± 2.1	14.0–22.9
Water depth below nest (cm)	44.8 ± 17.6	15.0–78.5
Above-water height of white mangrove (m)[a]	1.9 ± 0.6	1.0–3.7
Greatest breadth of white mangrove (m)[b]	3.9 ± 1.1	1.5–5.8
Distance to nearest white mangrove (m)[c]	3.2 ± 2.4	0.0–8.5
Distance to nearest shoreline (m)	48.4 ± 26.0	10.4–98.1
Distance to nearest active nest (m)	60.4 ± 59.6	18.7–308.2
Distance to nearest active nest (m)[d] (excluding three isolated nests)	42.7 ± 13.5	18.7–60.2
Distance to nearest active or inactive nest (m)	42.3 ± 59.9	10.2–283.9
Distance to nearest active or inactive nest (m)[d] (excluding three isolated nests)	23.1 ± 11.3	10.2–50.5

[a] One outlier excluded (dead white mangrove: nest 17; height <20 cm).

[b] Two outliers excluded (one dead white mangrove and one live white mangrove: nests 17, 21; breadth not measured and = 55.7 m, respectively).

[c] One outlier excluded (live white mangrove: nest 22; distance = 127.9 m).

[d] One isolated nest excluded from each of early, middle, and late nesting periods (nests 7, 13, and 17).

looked during the late period (date of clutch initiation was later than 19 May). The largest single brood observed comprised five young (from a mixed pair), and there were six broods (from four mixed pairs and two Caribbean Coot pairs) with four young. Reproductive success was 27%, and fledging success was 41.3%.

Nests were built along the water line in partially submerged, small, live white mangroves (*Laguncularia racemosa*; Table 1). Most nests were placed either in the central crotch (early and middle periods) or in smaller crotches of outside branches (late period); two nests during the late period were also placed either on remnants of dead white mangroves under live vegetation or on unconcealed dead white mangroves. All nests during the early and middle periods had short or long ramps, while only two nests during the late period had ramps. Nests were in isolated manglars (n = 18) or in rows of manglars (n = 4), but away from mangroves that formed the outer fringes of Southgate Pond's vegetated shoreline. Nests were located close to nest materials, the bulk of which (excluding sticks and twigs of mangroves) consisted of shoreline sea purslane (*Sesuvium portulacastrum*), a perennial succulent forb also used to construct most of the ramps. Seed pods of *Sesbania sericea*, a short-lived shrub, composed the inner nest lining of several nests. The dominant submerged plant (forb) of Southgate Pond was widgeon grass (*Ruppia maritima*), but this species was not used as nest material. Most manglars, both white and black (*Avicennia germinans*) mangroves, were located at the east end of the pond, where most nests were concentrated (Fig. 1). Two rather isolated nests (7, 13) were near the southwestern shoreline, and the most isolated nest (17) was near the northwestern shoreline. The density of coot nests during the three periods was 0.39–0.45 nests/ha.

Mean water depth at nests was 44.8 cm (Table 1) and declined throughout the breeding season (early period: 65.6 cm ± 11.0; middle period: 42.1 cm ± 3.8; late period: 29.0 cm ± 9.5; Kruskal-Wallis H = 15.14, $P < 0.001$; Fig. 2). Early nests were also farther away from the shoreline than middle or late nests (early period: 70.0 m ± 29.7; middle period: 49.6 m ± 11.2; late period: 28.5 m ± 15.8; Kruskal-Wallis H = 8.81, P = 0.010). Other comparisons of nest or nest-site variables between early, middle, and late periods were not significantly different.

Vegetation sampled at random points along line transects composed 34.6% (n = 151) of breeding habitat; the remainder was open water (n = 285), where mean water depth was significantly greater than in vegetated areas (open water: 45.8 cm ± 27.3; vegetation: 37.4 cm ± 26.2; t = 3.11, df = 434, P = 0.002). Live white and black mangroves and dead

FIG. 1. The location of 22 coot nests at Southgate Pond, St. Croix, U.S. Virgin Islands, during winter and spring of 2003–2004.

white mangroves dominated vegetation types within breeding habitat, and mean water depths at dead and live white mangroves were significantly deeper than at black mangroves ($F_{2,134} = 8.28$, $P < 0.001$; Table 2). Mean water depths at live white mangroves with and without coot nests were similar (without nests: 39.3 cm ± 25.7; with nests: 44.8 cm ± 17.6; Mann-Whitney $U = 434.5$, $P = 0.24$).

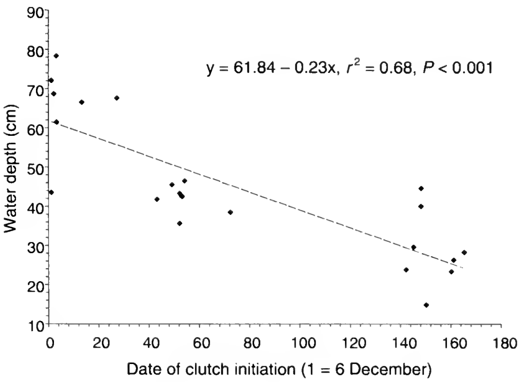

FIG. 2. Relationship between water depth below 22 coot nests and the date of clutch initiation at Southgate Pond, St. Croix, U.S. Virgin Islands, during winter and spring of 2003–2004.

Freshwater ponds.—Since 2002, 1–3 pairs of Caribbean Coots and mixed pairs have bred intermittently year-round at seven man-made, freshwater ponds on St. Croix, which range in size from 0.1 to 2.9 ha. The mean coot density at all sites combined for all breeding sequences over the 4 years was 4.2 pairs/ha (range = 0.3–10.0, $n = 17$) and apparent hatching success was high (16 of 24 nests based on hatch rates of the proportion of nests found). Most breeding records occurred after the 50-year rainfall event of mid-November 2003 filled the ponds. This event followed a dry period, when a variety of plant species had colonized the bottom of many dry, or nearly dry, ponds. In addition, the Virgin Islands Agricultural Station Middle Pond (see McNair 2006 for list of pond names and their locations on St. Croix) was deliberately drained during winter 2002–2003. Water levels varied between years at several sites when nesting occurred, espe-

TABLE 2. Mean water depth (cm) for eight vegetation types at Southgate Pond, St. Croix, U.S. Virgin Islands, during winter and spring of 2003–2004.

Vegetation type	*n*	Mean ± SD[b]
Dead *Laguncularia racemosa*	54	45.4 ± 26.9 A
Live *Laguncularia racemosa*	48	39.3 ± 25.7 A
Live *Avicennia germinans*	34	23.2 ± 21.2 B
Dead *Avicennia germinans*	3	38.6 ± 20.6[c]
Sesbania sericea	4	43.9 ± 17.0[c]
Sesuvium portulacastrum	4	27.8 ± 28.8[c]
Sesuvium portulacastrum on dead *L. racemosa*	2	52.7 ± 20.2[c]
Sporobolus virginicus[a]	2	6.8 ± 29.1[c]
All vegetation	151	37.4 ± 26.2
Open water	285	45.8 ± 27.3

[a] Seashore rush grass.

[b] Overall $F_{2,134} = 8.28$, $P < 0.001$; rows with different letters (A, B) are significantly different (Tukey's unequal *n* HSD *post-hoc* tests: $P = 0.026$ for live *Avicennia germinans* versus live *Laguncularia racemosa*; $P < 0.001$ for live *A. germinans* versus dead *L. racemosa*).

[c] Sample size too small to test.

cially at the Virgin Islands Agricultural Station Middle Pond. Live creeping burrhead (*Echinodorus berteroi*) was almost absent there in 2004, when the pond was not used by coots and emergent vegetation was restricted to the shoreline when the water level was higher. Although coots nested in a variety of live (five species) and dead (two species) vegetation, woody (especially remnant *S. sericea*, at four ponds) vegetation rather than perennial herbaceous vegetation was the predominant nest substrate (18 of 27, 67%). Nests ranged from 4 to 33.5 m away from the shoreline, and water depths below nests were generally greater for nests built in woody vegetation, especially *S. sericea* (usually 1.25–2.25 m). The bulky, conspicuous nests composed of sticks of *S. sericea* (~90 × 65 cm) were superficially shaped like the above-water portion of a beaver lodge. Anthropogenic disturbance at these seven ponds was negligible except around Carlton North Pond, where all vegetation except that fringing the shoreline was cleared for a housing development in early October 2004; however, coots continue to breed at Carlton North Pond.

DISCUSSION

Because of a drought on St. Croix that began in 2002, the bottom of Southgate Pond was dry in 2003 until water from heavy rains began to fill the pond in late August. Nonetheless, the basin was only about one-quarter full until a 50-year rainfall event during 10–14 November 2003 caused Southgate Pond to overflow. Coots colonized the pond and began laying eggs within 2–3 weeks after this seasonal wetland filled with water, typical of coots after arrival on their breeding grounds (Alisauskas and Arnold 1994).

When conditions are suitable, Southgate Pond is probably the preferred breeding site for coots on St. Croix (and in the USVI; McNair 2006), even though freshwater ponds, each with a small number of birds, support higher breeding densities (this study). Although Southgate Pond is brackish, the number of breeding pairs during three consecutive periods from December to May did not decline as salinity increased from low to moderately brackish; elsewhere, breeding densities typically decline as salinity increases (Kantrud 1985, Arnold 1993). Regardless, semi-permanent or seasonal wetlands are generally preferred habitat for American Coots in North America (Kantrud 1985, Arnold 1993, Alisauskas and Arnold 1994). Nests at Southgate Pond, which generally lacked emergent herbaceous vegetation, were built in woody vegetation. In Saskatchewan, small, isolated, partially submerged willow (*Salix* spp.) clumps were used as nest sites for a substantial percentage (22%) of American Coot nests during a wet year (Sugden 1979), although willows were not used as nest materials. This is different from what we observed at Southgate Pond, where white mangroves served as nest sites and as nest-building material; remnant or live woody plants (especially remnant *S. sericea*) at freshwater ponds on St. Croix were used similarly. In another Saskatchewan study, coot nests were composed of the same plant species that provided support for the nest (cf. Sutherland and Maher 1987).

Water depths below many nests in freshwater ponds on St. Croix were much deeper than water depths below nests in white mangroves at Southgate Pond. Apart from Southgate Pond, the most suitable freshwater breeding site for coots on St. Croix has been Granard South Pond, where three pairs nested in remnant *Sesbania* and other nest sites. Unlike mangroves at Southgate Pond, suitable remnant woody vegetation at freshwater ponds usually becomes available only when these ponds dry up and then refill with water, which kills the colonizing shrubs. Emergent vegetation suitable for nests at some of these ponds can be scarce, even when water levels are low. Nests in perennial emergent forbs were floating platforms built amongst this vegetation, which is typical of coot nests in marshes (Fredrickson 1970, Sugden 1979, Gorenzel et al. 1982, Kantrud 1985, Post 1990, Alisauskas and Arnold 1994, Frost and Massiah 2001).

At Southgate Pond, water depths at coot nests during each period were typical of those observed at American Coot nests on the North American mainland (Sugden 1979, Gorenzel et al. 1982, Sutherland and Maher 1987, Post 1990, Arnold 1993), although depths during the third period were rather shallow. Even though coots on the North American mainland frequently nest in residual emergent vegetation (Gorenzel et al. 1982, Alisauskas and Arnold 1993), in our study they probably avoided using dead white mangroves as nest sites in deeper water at Southgate Pond because nests in these sites would have been exposed. Were it not for the effects of hurricanes Hugo and Marilyn in 1989 and 1996, which killed many white mangroves farther from shore, several more pairs of coots may have used these mangroves as nest sites. Coots also avoided nesting in black mangroves, which are generally located closer to shore than the live white mangroves they used. Water depths at nests in white mangroves during the late period were similar to mean depths at black mangroves, suggesting that water depth at black mangroves was otherwise acceptable to coots. However, coots generally prefer deeper water farther from shore (Sutherland and Maher 1987, Post 1990, Arnold 1993). Furthermore, white mangroves offer superior structural support for nests (black mangroves lack the sturdy bowl-shaped central crotch and low lateral branches) and greater concealment. For similar reasons, American Coots in Saskatchewan nested in live willows but not quaking aspens (*Populus tremuloides*) (Sugden 1979).

As water levels declined, nest-site selection changed; by the late period, the central crotches of white mangroves were no longer suitable (too far above water). Nonetheless, inter-nest distances remained similar during all three periods, suggesting that territory sizes (which were not measured) also remained similar. Inter-nest distances between simultaneously active (or inactive) nests during all three periods were typical of those observed for coots elsewhere, although published data are unavailable for nests limited to woody vegetation. Unlike what has been observed at many North American sites characterized by emergent vegetation, coots at our study site built few non-nesting platforms (six in white mangroves), and the distribution and structure of nesting cover at Southgate Pond did not change over the breeding season. Given the fixed number of live white mangroves as potential nest sites for coots at Southgate Pond, territorial behavior probably prevented any additional coot pairs from breeding at the site. The location of coot nests is mainly controlled by territorial spacing, distance from shore, and the distribution and structure of nesting cover (Gullion 1953, Sugden 1979, Sutherland and Maher 1987). Water depth, although correlated with distance from shore in this study, was probably a less important factor in nest-site selection.

Nest concealment in woody vegetation must have been effective because hatching success at Southgate Pond was high. Apparent hatching success was also high at freshwater sites, which is typical of American Coots (Gorenzel et al. 1982, Alisauskas and Arnold 1994, Brisbin et al. 2002). Intraspecific nest parasitism was not observed at Southgate Pond or at the freshwater ponds. Fledging success at Southgate Pond, although not consistently associated with differences in water depth, was low (<41%). This contrasts with apparent fledging success at freshwater sites (this study), and that in North America, which is generally high (>50%; Alisauskas and Arnold 1994). Most broods observed at Southgate Pond consisted of 2–3 birds, lower than the number typically observed at freshwater ponds (7 of 13 broods had ≥4 fledged young). Thus, we speculate that brood losses within 5 days after hatching exceeded 50% at Southgate Pond. Low survivorship of young also occurred during the early brood period for White-cheeked Pintails (*Anas bahamensis*) at Humacao, Puerto Rico (F. J. Vilella pers. comm.), where most losses were attributed to rats (*Rattus* spp.), Great Egrets (*Ardea alba*), and Black-crowned (*Nycticorax nycticorax*) and Yellow-crowned (*Nyctanassa violacea*) night-herons. All of these potential predators were present at Southgate Pond.

Despite low reproductive success at Southgate Pond, the long intervals between breeding periods and the similar number of pairs breeding during each period suggest that some middle and late period nests were probably second or third broods rather than renests. Presumed success of second nesting attempts also occurred at three of the seven freshwater ponds. Nesting during the late period at Southgate Pond appeared to be possible because of heavy rainfall that occurred from 16 to 17 April, when water levels rose 17 cm, allowing coots to reset their breeding clock despite an overall drop in water level (14 cm) since the middle breeding period. Before the 50-year rainfall event of mid-November 2003, coots probably last nested at Southgate Pond in 2001, following the previous torrential rainfall event of 8 May when water filled the pond (CCB unpubl. data). This opportunistic, multibrooded breeding response to aquatic periods resulting from torrential vernal and autumnal rainfalls in an otherwise semi-arid environment may allow coots to overcome generally low reproductive success on St. Croix. Nevertheless, three breeding periods during one aquatic phase is probably exceptional (DBM and CCB unpubl. data). How frequently and successfully coots breed at Southgate Pond and freshwater sites on St. Croix in the future is currently being determined through an ongoing wetlands bird-monitoring scheme.

Management recommendations.—Southgate Pond (now part of the Southgate Coastal Reserve owned by the St. Croix Environmental Association) remains favorable habitat for nesting coots, even though environmental degradation has diminished this brackish pond to <50% of its original size (Gaines 2004, Gaines and Gladfelter 2004). The most difficult task at Southgate Pond is to maintain appropriate water levels for coot nest initiation during seasons and years when rainfall is insufficient. We endorse Gaines and Gladfelter's (2004:54–56) two major recommendations for water management to prolong the aquatic phase of Southgate Pond: (1) divert water into the pond, and (2) raise the maximum water depth from ~103 to ~138 cm. Manipulation of water levels should favor nesting coots and other wetland birds, although it may eliminate species that nest in terrestrial sites. During its dry phase, two species of conservation concern on St. Croix may nest at Southgate Pond: Wilson's Plover (*Charadrius wilsonia*) and Least Tern (*Sterna antillarum*). However, both species breed at more than 10 sites and are not as rare as coots. Furthermore, Southgate Pond is the best-documented site for coots in the eastern Caribbean (McNair 2006). When water levels are sufficient, the brackish habitat at Southgate Pond may be similar to that of brackish impoundments along the northern Gulf coast of the United States (e.g., an abundance of sea purslane and widgeon grass), where coots are abundant (Swiderek et al. 1988).

At the seven man-made, freshwater ponds, piped water is generally the best management option to maintain stable, generally high water levels. The most suitable freshwater site in the eastern Caribbean (Barbados) is man-made Marshall's Pond, which is dominated by *Echinodorus berteroi* (Frost and Massiah 2001; M. D. Frost pers. comm.), the herbaceous species used most frequently for nest sites on St. Croix. Maintaining stable water levels at the best site on St. Croix (Granard South Pond), as well as at the other ponds, should generally favor *E. berteroi* and other species with similar vegetative characteristics. Woody vegetation would no longer compose the dominant nest sites because stable water levels would generally prevent woody plants such as *S. sericea* from becoming established except along the immediate shorelines of these ponds.

Caribbean Coot systematics.—The taxonomic status of the Caribbean Coot requires further investigation (Roberson and Baptista 1988; also Gullion 1951, Phillips 1967, Payne and Master 1983, Clark 1985, Taylor 1996). Apparent non-assortative pairing of coots prevailed at Southgate Pond, where both types of coots occurred. One-half of the pairs at freshwater sites on St. Croix were paired non-assortatively. Furthermore, at least some mixed pairs successfully raised young, especially at Southgate Pond, indicating that the two types of coots can produce viable offspring (Gill 1964, Payne and Master 1983, Bond 1984). Thus, American and Caribbean coots may compose one species with variant, intergraded phenotypes of which A and E birds represent the extreme types. Although some birds can be individually recognized in the field, an accurate assessment of phylogenetic relationships and the taxonomic status of American and Caribbean coots will require studies based on morphological and genetic analyses along with observations of mating behavior and pair bonds of marked birds. This will also require confirming identification of shield characteristics and correlating them with other morphological measurements.

ACKNOWLEDGMENTS

The U.S. Fish and Wildlife Service provided partial financial support to the Division of Fish and Wildlife, U.S. Virgin Islands (Federal Aid Program, Pittman-Robertson Wetlands Project, W15). S. L. Fromer and L. D. Yntema shared their bird observations; A. G. Gaines contributed data on salinities at Southgate Pond and provided a digitized bathymetric map of this site; D. B. Nelthrop and D. M. Schuster, among other landowners, provided access to their freshwater ponds; J. A. Collazo and F. J. Vilella reviewed a penultimate draft of the manuscript, and T. W. Arnold, F. E. Hayes, and an anonymous individual reviewed earlier versions of the paper.

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The Wilson Journal of Ornithology 118(2):218–224, 2006

INSULAR AND MIGRANT SPECIES, LONGEVITY RECORDS, AND NEW SPECIES RECORDS ON GUANA ISLAND, BRITISH VIRGIN ISLANDS

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ABSTRACT.—We conducted mist netting each October from 1994 to 2004 on Guana Island, British Virgin Islands, and recorded bird sightings to develop a more complete inventory of the island's resident and migrant species. During our study, we recorded four new species for the British Virgin Islands: Magnolia Warbler (*Dendroica magnolia*; 1996), Golden-winged Warbler (*Vermivora chrysoptera*; 1997), Swainson's Thrush (*Catharus ustulatus*; 2000), and Red-necked Phalarope (*Phalaropus lobatus*; 2004). Blackpoll Warbler (*Dendroica striata*) was the most frequently captured Neotropical migrant landbird, despite only being first detected in the region in 1989. Captures and detections of other Neotropical migrant landbirds suggest that many species may be more common in the region than previously believed, or, as speculated by other researchers, that migrant routes may be shifting eastward due to habitat degradation on western Caribbean islands. We also used recapture data to establish longevity records of resident species, including Caribbean Elaenia (*Elaenia martinica*; ≥7 years), Bananaquit (*Coereba flaveola*; 7 years), Black-faced Grassquit (*Tiaris bicolor*; ≥9 years), and Zenaida Dove (*Zenaida aurita*; 5 years). Longevities of other resident species were similar to, or slightly less than, those reported elsewhere. *Received 22 February 2005, accepted 30 November 2005.*

Ornithological research conducted in the West Indies has covered an array of topics, including avian species occurrence and distribution, ecology of individual species, effects of hurricanes on island bird populations, migration patterns, and community dynamics (Wiley 2000). In the Virgin Islands region, researchers have addressed avifaunal occurrence and distribution (LaBastille and Richmond 1973, Mirecki et al. 1977, Norton et al. 1989), and species ecologies (Askins and Ewert 1991, Chipley 1991, Mayer and Chipley 1992, McNair et al. 2002); however, considerably less ornithological study has been conducted in the Virgin Islands—especially the British Virgin Islands (BVI)—than in other areas of the West Indies. In a bibliography consisting of 11,648 entries for ornithological work conducted in the West Indies from 1750 to 1994, only 7.5% of the entries included information for the Virgin Islands; only the extralimital islands of San Andres, Providencia, and the Swans have received less attention (Wiley 2000).

We conducted mist netting on Guana Island, BVI, each October from 1994 to 2004. To our knowledge, the Guana Island station is the only current and consistently operated banding station in the British Virgin Islands and one of only three in the eastern Caribbean (St. Martin and Barbados being the others). Previously, information from the island has proven important in developing a better understanding of Neotropical migrant bird use of the region during the autumn migration (McNair et al. 2002). However, our data on species frequency of occurrence, which could be helpful in this effort, have not been made available until now. For example, Faaborg and Terborgh (1980) considered the Red-eyed Vireo (*Vireo olivaceus*) as a rare transient migrant encountered only in the Greater Antilles. In a status review of migrant landbirds in the Caribbean, Arendt (1992) did not list Red-eyed Vireos as even occurring in the British Virgin Islands. Indeed, Norton (1996) noted an account of a Red-eyed Vireo in Puerto Rico as one of only a few confirmed records for the species on the Puerto Rico Bank. The regular occurrences of Red-eyed Vireos at Guana Island (CWB and FCS unpubl. data), however, suggest that the species uses the Virgin Islands as a migration stopover more than previously believed.

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Here, we present an account of resident and migrant species banded during October each year for 11 years on Guana Island. For some species, we report longevity records based on recaptures of banded individuals. Additionally, we provide accounts of new or rarely reported species based on both banding and site records.

METHODS

The Virgin Islands, including both the U.S. Virgin Islands and the BVI, are a chain of approximately 76 islands and cays located 100–150 km east of Puerto Rico. Guana Island (18° 30′ N, 64° 30′ W) lies immediately north of Tortola, the largest of the BVI islands. Within the BVI, Guana Island is relatively small (3 km^2) compared with other inhabited islands, such as Tortola (54 km^2), Virgin Gorda (21 km^2), and Jost Van Dyke (10 km^2). The BVI has a subtropical climate tempered by northeasterly trade winds, with temperatures normally ranging from 28 to 33° C, and fairly constant humidity levels (~78%) throughout the year (Lazell 2005). Annual mean rainfall for Guana Island is estimated at 92 cm (Lazell 2005), but data are limited and the long-term average may be lower.

Guana Island is topographically rugged, with elevations ranging from sea level to 246 m. Approximately 90% of the island is covered by subtropical dry forest, with ghut forests (mesic forest; 5%) present in some drainages; miscellaneous covers include human-altered areas (3%), mangroves (1%), and beach (1%) (Lazell 1996; CWB unpubl. data). Lazell (1996) lists the primary native vegetation on Guana Island as 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 (*Leucaena leucocephela*) is common in disturbed areas. Introduced species include coconut (*Cocos nucifera*), tamarind (*Tamarindus indica*), and royal poinciana (*Delonix regia*).

We operated a mist-netting station each October from 1994 to 2004. Nets were located primarily along a northeast–southwest ridge and southeast-facing slope of a mountain on the island's west side. The majority of nets were in subtropical dry forest areas, but each year we placed 2–3 nets in human-altered areas along the ridge, all at approximately 100-m elevation. For one afternoon each year, we also netted along the shore of a salt pond to sample the shorebirds present. We attempted to use the same net locations each year, but during the earlier years of the project we conducted some "exploratory netting" in other areas. Duration of mist-netting operations and number of nets operated were subject to local weather conditions, the number of assistants available, and the amount of time we were allowed access to the island by its owners; thus, the number of nets used (mean = 8.1 ± 0.9 SE) and mist-netting days (mean = 8.8 ± 1.3 SE) varied annually. Weather permitting, nets were opened at 06:30 AST and closed between 10:00 and 11:00; occasionally, mist-netting was also conducted in the afternoon.

We identified all birds captured to the species level, and, when possible, determined their sex and age (Raffaele 1989, Pyle 1997, Raffaele et al. 2003). We recorded weight (g), length of wing chord (mm), and banded each bird with a federal aluminum leg band. We did not conduct systematic avian surveys (e.g., point counts), but we did record species encountered while engaged in other studies and activities on the island. Combined, our observation records and mist-netting efforts allowed us to compile an annual species list for the island and document occurrences of species previously unrecorded on the island and/or the BVI. We compiled recapture records to determine longevity for both resident and migrant species. We considered all after-hatching-year birds (AHY) to be 1 year old at time of initial capture.

RESULTS

Banding.—We conducted mist netting for a mean of 252 ± 53 SE net-hr each October from 1994 through 2004. During the study period, we captured 1,410 birds, 188 (13%) of which were recaptures of birds banded in previous years (Table 1). These numbers do not include captures of birds that we did not band, such as the Green-throated Carib (*Eulampis holosericeus*) and the Antillean Crested Hummingbird (*Orthorhyncus cristatus*). We captured 44 species, the most common of which was the resident Bananaquit (*Coereba flaveola*; 676 captures). Other frequently captured

TABLE 1. Species and numbers of birds captured and banded at Guana Island, British Virgin Islands, 1994–2004.

Species	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	*n*	Percent recaptured
American Kestrel (*Falco sparverius*)	0	0	1	0	4	0	0	0	1	4	0	10	10
Wilson's Plover (*Charadrius wilsonia*)	0	0	8	0	3	10	2	2	1	0	2	28	29
Semipalmated Plover (*Charadrius semipalmatus*)	0	0	0	0	0	0	1	0	0	1	1	3	0
Black-necked Stilt (*Himantopus mexicanus*)	0	0	0	7	0	2	1	2	0	0	0	12	8
Lesser Yellowlegs (*Tringa flavipes*)	0	0	2	0	0	1	0	0	1	0	1	5	0
Solitary Sandpiper (*Tringa solitaria*)	0	0	0	0	0	0	1	0	0	0	0	1	0
Spotted Sandpiper (*Actitis macularius*)	0	0	6	2	2	2	0	0	0	0	3	15	7
Ruddy Turnstone (*Arenaria interpres*)	0	0	0	1	5	2	0	0	3	3	0	14	0
Semipalmated Sandpiper (*Calidris pusilla*)	0	0	2	0	2	3	2	1	1	0	1	12	0
White-rumped Sandpiper (*Calidris fuscicollis*)	0	0	0	0	0	0	0	0	0	2	0	2	0
Stilt Sandpiper (*Calidris himantopus*)	0	0	0	1	0	0	0	0	0	0	0	1	0
Scaly-naped Pigeon (*Patagioenas squamosa*)	0	0	0	0	1	0	0	0	0	0	0	1	0
Common Ground-Dove (*Columbina passerina*)	1	0	9	1	9	0	0	5	1	1	0	27	11
Zenaida Dove (*Zenaida aurita*)	0	1	3	4	8	5	0	26	4	1	5	57	14
Yellow-billed Cuckoo (*Coccyzus americanus*)	0	0	0	0	0	0	0	1	0	0	0	1	0
Mangrove Cuckoo (*Coccyzus minor*)	0	0	1	0	1	0	0	1	0	0	2	5	0
Caribbean Elaenia (*Elaenia martinica*)	0	4	5	4	11	0	0	7	1	6	5	43	11
Gray Kingbird (*Tyrannus dominicensis*)	0	0	0	0	3	0	0	7	1	0	0	11	0
Yellow-throated Vireo (*Vireo flavifrons*)	0	0	0	0	0	0	0	0	0	1	0	1	0
Red-eyed Vireo (*Vireo olivaceus*)	0	1	2	1	2	0	0	1	0	1	4	12	0
Swainson's Thrush (*Catharus ustulatus*)	0	0	0	0	0	0	1	0	0	1	0	2	0
Pearly-eyed Thrasher (*Margarops fuscatus*)	3	0	21	2	13	5	1	21	0	12	15	93	4
Golden-winged Warbler (*Vermivora chrysoptera*)	0	0	0	1	0	0	0	0	0	0	0	1	0
Northern Parula (*Parula americana*)	0	0	2	0	0	0	0	0	0	0	2	4	0
Yellow Warbler (*Dendroica petechia*)	0	0	0	0	0	1	0	0	0	0	0	1	0
Magnolia Warbler (*Dendroica magnolia*)	0	0	1	0	0	0	0	0	0	1	1	3	0
Cape May Warbler (*Dendroica tigrina*)	0	1	0	0	0	0	0	0	0	0	0	1	0
Black-throated Blue Warbler (*Dendroica caerulescens*)	0	0	2	0	0	0	0	0	0	0	0	2	0
Blackpoll Warbler (*Dendroica striata*)	0	11	27	9	83	0	5	16	8	19	7	185	0
Black-and-white Warbler (*Mniotilta varia*)	0	0	4	0	1	0	0	0	0	2	0	7	0
American Redstart (*Setophaga ruticilla*)	0	0	0	0	1	0	0	0	1	0	0	2	0
Worm-eating Warbler (*Helmitheros vermivorum*)	0	0	0	0	0	0	0	0	0	1	0	1	0
Ovenbird (*Seiurus aurocapilla*)	0	0	0	0	3	0	0	0	0	2	1	6	0
Northern Waterthrush (*Seiurus noveboracensis*)	0	0	3	0	2	0	0	0	0	0	0	5	0
Kentucky Warbler (*Oporornis formosus*)	0	0	1	0	0	0	0	0	0	1	1	3	0
Hooded Warbler (*Wilsonia citrine*)	0	0	0	0	0	0	0	0	0	1	0	1	0
Bananaquit (*Coereba flaveola*)	12	68	50	85	145	9	16	131	45	72	43	676	20
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0	1	0	0	0	0	0	0	0	1	0	2	0
Indigo Bunting (*Passerina cyanea*)	0	0	1	0	0	0	0	0	0	1	3	5	0
Black-faced Grassquit (*Tiaris bicolor*)	11	6	26	9	18	2	11	16	8	11	30	148	13
Lesser Antillean Bullfinch (*Loxigilla noctis*)	0	0	0	0	1	0	0	0	0	0	0	1	0
Totals	27	93	177	128	317	42	41	237	76	145	127	1,410	

TABLE 2. Longevity records for species ≥4 years old on Guana Island, British Virgin Islands, 1994–2004.

Species	Age[a]	Sex	Year captured	Last recapture	No. of recaptures	Minimum age (years)
Wilson's Plover	AHY	F	1996	1999	2	4
	AHY	M	1996	1999	1	4
	AHY	U	1996	1999	1	4
	AHY	M	1996	1999	2	4
Black-necked Stilt	AHY	F	1997	2001	1	5
Spotted Sandpiper	HY	U	1998	2004	2	6
Common Ground-Dove	AHY	F	1998	2001	1	4
Zenaida Dove	AHY	M	1997	2001	2	5
	AHY	M	1998	2001	1	4
	AHY	M	2001	2004	1	4
Caribbean Elaenia	Unk	U	1996	2003	1	7
	Unk	U	1996	2001	1	5
Pearly-eyed Thrasher	AHY	U	1998	2001	1	4
Black-faced Grassquit	AHY	F	1996	2004	2	9
	AHY	F	1998	2004	1	7
	AHY	M	1998	2003	1	6
	HY	U	1998	2003	1	5
	AHY	F	2000	2004	2	5
	AHY	M	1996	2000	1	5
Bananaquit	AHY	M	1995	2001	3	7
	AHY	M	1997	2003	2	7
	HY	F	1998	2004	2	6
	AHY	M	1998	2002	2	5
	AHY	M	1997	2001	2	5
	AHY	F	1997	2001	1	5
	HY	M	1998	2003	2	5
	AHY	M	2001	2004	3	5
	AHY	M	1997	2000	1	4
	AHY	M	1995	1998	2	4
	AHY	M	1995	1998	3	4
	HY	F	1997	2001	2	4
	AHY	M	2000	2004	2	4
	AHY	M	2001	2004	2	4
	AHY	M	1994	1997	2	4
	HY	F	1998	2002	2	4
	HY	M	1998	2002	2	4
	AHY	M	1998	2001	1	4
	AHY	M	1998	2001	1	4

[a] AHY = after-hatching-year, HY = hatching-year, Unk = unknown age.

resident species were Black-faced Grassquit (*Tiaris bicolor*; 148 captures) and Pearly-eyed Thrasher (*Margarops fuscatus*; 93 captures). These three species are among the most abundant residents on Guana Island. We also captured 20 species of Neotropical migrant landbirds, the majority of which were warblers (Table 1). The Neotropical migrant captured most frequently was the Blackpoll Warbler (*Dendroica striata*; 185 captures), followed by the Red-eyed Vireo (12 captures, multiple additional sightings). Other Neotropical migrants encountered included many species (e.g., Yellow-throated Vireo, *Vireo flavifrons*; Table 1) previously reported only from the western Greater Antilles or for which there were no records from the BVI or the Lesser Antilles (Faaborg and Terborgh 1980, Arendt 1992).

Longevity.—We determined longevity for all species recaptured on the island, and provide data for those older than 3 years (Table 2). Among shorebirds, the longevity records were 5 years for Black-necked Stilt (*Himantopus mexicanus*), 6 years for Spotted Sandpiper (*Actitis macularius*), and 4 years for

Wilson's Plover (*Charadrius wilsonia*); however, our recapture rate for these species was low and we suspect that our longevity estimates, especially for the resident Wilson's Plover, may be substantially lower than actual longevity. Among Columbiformes, our longevity records were 4 years for Common Ground-Dove (*Columbina passerina*) and 5 years for Zenaida Dove (*Zenaida aurita*). Among resident passerines, we recaptured Caribbean Elaenias (*Elaenia martinica*) that were ≥7 and ≥5 years old, and we recaptured a 4-year-old Pearly-eyed Thrasher. Among the 19 recaptured Bananaquits, two were 7 years old, one was 6 years old, and the others were 5 and 4 years old. The oldest bird recaptured was a ≥9-year-old female Black-faced Grassquit; we also recaptured one 6-year-old and three 5-year-old grassquits.

New species records.—During the course of our netting operations and surveys, we obtained species records for Guana Island and, in some cases, the British Virgin Islands. Our captures of a Magnolia Warbler (*Dendroica magnolia*) in 1996 and a Golden-winged Warbler (*Vermivora chrysoptera*) in 1997 were first records for the BVI. More significant, however, was our capture of a Swainson's Thrush (*Catharus ustulatus*) in 2000, the first record for the Virgin Islands and only the second from east of Cuba (McNair et al. 2002). In 2003, we captured another Swainson's Thrush and obtained a visual sighting of a second, unbanded individual. Finally, our observation of a hatching-year Red-necked Phalarope (*Phalaropus lobatus*) on the salt pond of Guana Island in October 2004 represented a first record for that species in the Virgin Islands.

DISCUSSION

Deriving longevity estimates from survivorship models is preferable to using simple longevity records (Krementz et al. 1989). The reliability of survival estimates, however, depends upon robust recapture data (e.g., Burnham et al. 1987), which often are not available for many species. Longevity records, therefore, are still valuable for providing some basic life-history information on little-studied species. This may be especially true for island settings, where longer-lived species are at lower risk of localized extinction (Newton 1998). Although longevity records have been reported for many North American bird species (e.g., Kennard 1975, Klimkiewicz et al. 1983), little information is available on the life spans of tropical birds (Snow and Lill 1974, Faaborg and Winters 1979, Johnston et al. 1997). The few Caribbean bird species for which there are longevity records are primarily Puerto Rican (Faaborg and Winters 1979, Woodworth et al. 1999), and there is virtually no published information on the longevity of birds in the eastern Caribbean. Thus, our data provide new age records for several Caribbean species. In Puerto Rico, Faaborg and Winters (1979) recaptured 36 of 219 Bananaquits, the oldest of which was 4 years and 7 months. Outside of the Caribbean, de Souza Lopes et al. (1980) reported a 4-year, 8-month-old Bananaquit from their study in Brazil. Our longevity record of 7 years for Bananaquits exceeds previous reports by a minimum of 2 years. Furthermore, our Bananaquit data suggest that ages of 4 and 5 years are not uncommon. Perhaps most unusual is our 9-year-old age record for a Black-faced Grassquit, with additional individuals aged 6 and 5 years. These far exceed the previous report of 2 years and 11 months (Faaborg and Winters 1979). The 4-year-old Common Ground-Dove in our study is similar to the longevity records of 4 years and 4 years and 1 month from Puerto Rico (Faaborg and Winters 1979). However, the 5-year, 5-month-old Pearly-eyed Thrasher reported by Faaborg and Winters (1979) exceeds our oldest known thrasher by 1 to 2 years. We found no reports of longevity for Caribbean Elaenia with which to compare our records; however, our records of 7- and 5-year-old Caribbean Elaenia are similar to those reported for unspecified *Elaenia* spp. in Brazil (6 years and 3 months, and 5 years; de Souza Lopes et al. 1980) and substantially exceed ages recorded for Yellow-bellied Elaenia (*E. flavogaster*; 2 years and 11 months) and Mountain Elaenia (*E. frantzii*; 3 years and 9 months) in Panama (Loftin 1975). We believe that the 5-year-old Zenaida Dove from our study also represents a longevity record for that species, as we could find no reports with which to compare our data.

Many of the Neotropical migrants captured or sighted during our study are known to occasionally occur in the BVI. Some of our sightings and captures, such as Hooded Warblers (*Wilsonia citrina*) and Worm-eating Warblers (*Helmitheros vermivorum*), are unusual for the BVI. Still others, including Magnolia Warbler, Golden-winged Warbler, Swainson's Thrush, and Red-necked Phalarope, provide new records for the BVI. Detections of Swainson's Thrush and Red-necked Phalarope were particularly interesting. Within the Caribbean region, Raffaele et al. (2003) indicated that Swainson's Thrush was found only rarely in the western Greater Antilles and only during migration; thus, detections of Swainson's Thrush in 2 different years on Guana Island was notable. Raffaele et al. (2003) also indicated that Red-necked Phalarope is a very rare migrant in the Bahamas, Cuba, and Hispaniola (e.g., Greater Antilles); in Puerto Rico, the species has been recorded only twice (Raffaele 1989). In September 2003, however, a Red-necked Phalarope was reported on Guadaloupe Island (Norton et al. 2003), which lies 400 km southeast of Guana Island.

Our detections of Blackpoll Warbler and Red-eyed Vireo, and our consistent detections of other, less common species—such as Yellow-throated Vireo, Swainson's Thrush, Indigo Bunting (*Passerina cyanea*), and numerous warbler species—indicate that they may be more common in the eastern Caribbean during migration than previously believed due to a lack of searching or banding efforts in that region. For example, Blackpoll Warbler, the most common warbler encountered on Guana Island and the second-most frequently captured species overall, was not reported in the BVI until 1989 (Norton 1990); it had been considered a common Neotropical migrant through the Greater Antilles but uncommon to rare on other islands (Arendt 1992, Raffaele et al. 2003). Similarly, Red-eyed Vireo was thought to be very uncommon or vagrant in the Lesser Antilles (Faaborg and Terborgh 1980, Arendt 1992, Norton 1996, Raffaele et al. 2003); however, our regular sightings and captures of Red-eyed Vireos suggest that the species may be a more common migrant in the BVI than previously believed.

Overall, our detections of species previously believed to be uncommon or not present within the BVI may have been due to a lack of field surveys and banding efforts throughout most of the Virgin Islands and Lesser Antilles. Alternatively, our detections may be related to changes in habitat conditions in the western Caribbean islands. As habitat availability decreases in the western islands, some migrant species might be shifting their migration routes eastward (Arendt 1992). Regardless of possible shifts in migration routes, it appears that Guana Island—a functional ecosystem protected as a nature preserve (Lazell 1996)—provides important habitat for both resident and transient migrant species. A low-occupancy, private resort occupies less than 2% of the surface area of Guana Island; the remainder of the island is almost completely free of direct human impacts and exists in a near-natural state (Lazell 1996). Furthermore, exotic herbivores and carnivores, which are a severe problem throughout much of the Caribbean, occur at very low densities and are heavily controlled on the island.

As larger islands in the Virgin Islands (e.g., Tortola, St. John, Virgin Gorda) continue to undergo deforestation and development (e.g., Arendt 1992), smaller islands maintained in primarily natural states are likely to become increasingly important for conservation of both resident and migrant birds. However, small islands, such as Guana Island, may not provide a full range of landscape characteristics required for some migrant or wintering Neotropical songbirds. For example, Northern Parula (*Parula americana*) and American Redstart (*Setophaga ruticilla*), both common nonbreeding residents in the Virgin Islands (Raffaele et al. 2003), are seldom detected on Guana. Further examination of resource use and spatial needs of Neotropical songbirds migrating through or wintering in the BVI is needed to facilitate conservation efforts.

ACKNOWLEDGMENTS

We give our sincere thanks to G. Jarecki, H. Jarecki, and the staff of Guana Island for their support and facilitation of this research. We thank W. J. Arendt, A. Olivieri, G. Perry, O. Perry, J. Richardson, P. Sibley, A. Sutton, S. Valentine, and T. Willard for assisting with banding operations and other logistics. Support for the study was provided by The Conservation Agency through a grant from the Falconwood Foundation, and by the U.S. Geological Survey Texas Cooperative Fish and Wildlife Research Unit. This manuscript benefited from the reviews and constructive comments of G. Perry, R. L. Norton, and three anonymous reviewers.

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The Wilson Journal of Ornithology 118(2):225–236, 2006

REPRODUCTIVE BEHAVIOR OF THE YELLOW-CROWNED PARROT (*AMAZONA OCHROCEPHALA*) IN WESTERN PANAMA

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ABSTRACT.—We studied the breeding biology of the Panamanian subspecies of the Yellow-crowned Parrot, *Amazona ochrocephala panamensis*, during 1997–1999 in the province of Chiriquí, Panama, to provide basic information regarding the breeding behavior and reproductive success of these parrots in their natural habitat. We recorded parrot behaviors throughout the reproductive period, monitored nest success, and characterized occupied and non-occupied tree cavities. All breeding attempts involved a male-female pair. Clutch size ranged from 2 to 4 eggs, which were incubated only by the female, beginning when the first egg was laid. Incubation averaged 25 days and the eggs hatched asynchronously. During the incubation period, females remained inside the nest for long periods of time, though they often departed from the nest area during early mornings and late afternoons, presumably to forage; during this period, males were not observed entering the nest, though they often remained nearby. During the nestling period, males contributed significantly to feeding the offspring. Pairs nested in trees that were in good or fair condition, and did not favor cavities in any one tree species. As found in many other field studies of parrots, breeding success was low. Only 10% (1997–1998) and 14% (1998–1999) of the nests survived poaching and natural predation. Because nest poaching was the primary cause of breeding failure and poses a serious threat to population viability, we also present data on poaching techniques and the local trade of nestling parrots. Overall, the pool of breeding adults is likely made up of aging individuals that are not being replaced, setting the stage for a rapid population decline. *Received 13 January 2005, accepted 23 November 2005.*

The genus *Amazona* consists of 31 species distributed throughout the Neotropics (Juniper and Parr 1998); however, the breeding biology of only a few species has been studied (see below). Nest poaching and the capture of adult birds for the pet trade, together with habitat loss due to deforestation, have contributed to the precipitous decline of *Amazona* populations in Central America, South America, and the Caribbean region (Forshaw 1989, Juniper and Parr 1998, Wright et al. 2001). Like many of the eight other subspecies that form the Yellow-crowned Parrot complex (Juniper and Parr 1998, Eberhard and Bermingham 2004), *Amazona ochrocephala panamensis* has not escaped these pressures (Asociación Nacional para la Conservación de la Naturaleza 1995, Autoridad Nacional del Ambiente 1995a). In Panama, the population of this subspecies has declined considerably due to nest poaching (Ridgely 1981) and the loss of nesting habitat to agricultural and cattle-grazing activities (Autoridad Nacional del Ambiente 1995a, 1995b).

The breeding biology of a few *Amazona* species has been studied in the wild; many of these studies occurred on Caribbean islands (Snyder et al. 1987, Gnam 1991, Rojas-Suárez 1994, Wilson et al. 1995) while others provide information on mainland species (Enkerlin-Hoeflich 1995, Enkerlin-Hoeflich and Hogan 1997, Renton and Salinas-Melgoza 1999, and Seixas and Mourão 2002). Additional data on breeding behavior come from studies of captive *A. albifrons* (Skeate 1984) and *A. viridigenalis* (Wozniak and Lanterman 1984). Overall, the studies have revealed that females typically spend long periods inside the nest during the incubation and early nestling periods, and depend, at least to some degree, on being fed by their mates. Four *Amazona* species in Mexico apparently select nest sites based on tree species, size, cavity height, and entrance size (Enkerlin-Hoeflich 1995, Renton and Salinas-Melgoza 1999).

Wright et al. (2001) summarized data from many field studies and showed that nest poaching is a principal cause of reproductive failure in Neotropical parrots, with poaching rates being higher at mainland sites than on

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islands, and lower in protected areas (e.g., nature reserves). While the impact of nest poaching on parrot reproductive success is clear, there are few studies that provide information on specific techniques used by poachers.

To date, there have been no published studies of the reproductive behavior of *A. ochrocephala* in Panama or other parts of its range. Here, we report our observations of the species' breeding behavior, describe the characteristics of nest sites and nest trees, and quantify reproductive success during two breeding seasons. We also present data regarding the poaching techniques used in the study area.

METHODS

Study area.—Fieldwork was conducted during the dry season (December–April) of 1997–1998 and 1998–1999 in the lowlands of Corregimiento de San Juan (San Lorenzo district) of the province of Chiriquí in western Panama. The natural vegetation in the area is tropical dry forest (following Holdridge's [1967] life zone classification) and mangrove, but in many places it has been cleared for agriculture and cattle grazing. Annual rainfall is ~1,000 mm; mean annual temperature is ~30° C, with mean temperatures of 35° and 28° C during the dry and rainy seasons, respectively (Instituto de Recursos Hidráulicos y Electrificación 1998, 1999). The study area was located at ~8° 17′ 15″ N, 82° 3′ 10″ W and encompassed an area of ~8,800 ha; ~3,875 ha had been partially cleared for agriculture and cattle grazing (on haciendas Miraflores, El Tekal, and Los Asentamientos de San Juan), and the remaining 4,925 ha were mangrove. The partially cleared areas still contained remnant patches of tropical dry forest dominated by *Gliricidia sepium* and *Erythrina fusca* trees, the lower-statured *Curatella americana*, and palms belonging to the genera *Roystonea* and *Acrocomia* (Acosta 1996).

Characterization of nest sites.—During the first breeding season (1997–1998), we only studied nests found in the mangrove habitat; in the following season (1998–1999), we extended our nest monitoring to include those found in the partially cleared dry forest habitat. We found 21 active nests during the 1st year and 42 during the 2nd year. Of the nests found in the 2nd year, 14 had been used by parrots during the previous breeding season; therefore, to avoid pseudoreplication, our data on cavity and nest-tree characteristics represent 49 (and not 63) active nests. In the second breeding season, 20 of the nests were found in mangrove habitat, and the remaining 22 in the partially cleared dry forest.

To find nest cavities, we searched for trees with cavities, observed parrots flying and vocalizing in the area, and interviewed local residents and field laborers for information about nesting parrots. Nests were considered active if they contained *A. o. panamensis* eggs or nestlings.

To determine the availability of cavities, we searched for additional tree cavities near nest trees. By searching the area surrounding an occupied nest tree, we attempted to control for larger-scale habitat variation (e.g., vegetation density, canopy height, distance to feeding areas) that might have influenced cavity choice. All trees within 100 m of each nest tree were examined for the presence of large cavities (i.e., cavities similar in size to those occupied by parrots). For a given nest tree, two of the surrounding trees found to contain cavities were selected at random for inclusion in the sample of unoccupied cavities. If a selected tree contained more than one cavity, we selected one of them at random to provide data on cavity location and orientation. In the partially cleared dry forest habitat, we extended two of these searches beyond 100 m (108 and 116 m) in order to find trees with large cavities. Determining that a cavity was similar in size to occupied cavities was admittedly subjective; therefore, we do not present any analyses comparing the dimensions of occupied versus unoccupied cavities.

We used leaf, flower, and/or fruit samples to identify the genus and species (where possible) of trees containing cavities. For each cavity we measured horizontal and vertical width of the cavity opening, inside vertical depth and cavity diameter (measured at the cavity floor), and distance from the ground to the lower edge of the cavity opening (see Saunders et al. 1982). Measurements were made using a 30-m tape to a precision of 0.5 cm, and were used to calculate the areas of the cavity entrance and cavity floor. For each cavity, we noted its location relative to the tree's structure—branch (cavity completely contained within a branch), trunk (cavity completely contained within the main trunk), and branch/trunk (cavity at the intersection of a branch and the trunk). We determined the orientation of the cavity opening using a compass, and measured each tree's height using a clinometer. We classified the physical condition of each tree—good, fair, poor, or dead—using the scheme outlined by Sauad et al. (1991; see also Saunders et al. 1982).

Behavioral observations.—We monitored 63 nests during the two breeding seasons: 21 during 1997–1998 and 42 during 1998–1999. Of the 63 nests, 5 were selected each year for detailed behavioral observations of parrots (hereafter referred to as focal nests). In the first field season, focal nests were chosen at random; during the second field season, nests were selected on the basis of their accessibility.

We made preliminary observations early in the breeding season (prior to egg-laying) at each of the focal nests. An observation period lasted 13 hr (06:00 to 19:00 UTC-5). Each year, we watched three of the five focal nests for two preliminary observation periods, and the other two were watched for a single observation period. In most cases (9 of 16 observation periods), we conducted preliminary observations prior to capture of the focal individuals.

To identify the sex of focal individuals, we used nets (set up at dawn) to capture one or both members of each focal pair early in the field season (prior to the onset of breeding). We used nylon (4.5 × 15 m) and cotton (6 × 8 m) fishing nets (mist nets were not available) and suspended them using ropes and/or poles over the nest opening or across a flyway used by the birds. In both years, the sex of each captured individual was identified in the field by a veterinarian (R. De Obaldía) using a laparoscope. We then marked the female on the upper chest with Rhodamine B, so that she could be distinguished from the male in subsequent observations. Because the Rhodamine B marks faded after several weeks, the birds were subsequently marked passively by applying dye to the nest opening (see Eberhard 1998). This passive marking was done before the prior markings had faded completely, so that the identity of the newly marked birds was known. With this technique, the birds invariably marked themselves on different parts of the body with unique patterns, so the male and female could be distinguished from one another.

For the remainder of each focal pair's breeding attempt, we made behavioral observations at ~3-day intervals. We observed during 3-hr periods when the parrots were most active (either 06:30–09:30 or 15:45–18:45), following the methodology used in other parrot studies (e.g., Eberhard 1998, Renton and Salinas-Melgoza 1999). The results reported here are based on 859 hr of nest observation (208 hr were preliminary observations). We observed nests with the aid of binoculars from a distance of ~15 m (the parrots quickly habituated to the observer's presence). During each observation period, we noted the following: time spent by the adults inside the nest; time spent in the nest area (defined as being in visual range of the observer, which was approximately 50–75 m in the mangrove habitat and approximately 100 m in the partially cleared dry forest areas); number of other parrots traveling with the focal individual when approaching or departing; and presence of other humans in the nesting area. Other general observations (allofeeding, allogrooming, vocal and plumage displays, appearances of nestlings at the cavity opening, age at which young left the nest) were noted *ad lib.* When adults made short visits to the nest, presumably to feed young, we recorded total time in the nest cavity. Focal nest observations were made until 6 days after the last chick fledged, or 6 days after a nest was depredated or poached.

Three of the focal nests observed during the first breeding season (1997–1998) were in cavities that were re-occupied in the following breeding season, and were considered focal nests during the 2nd year of the study. Because it is possible that pairs used the same cavity in consecutive years, our data might include some year-to-year pseudoreplication in the focal-nest behavioral observations. The adults were not permanently marked, so it was impossible to determine whether this occurred.

For the analysis of behavioral data, we divided the breeding season into four stages: pre-laying, laying, incubation, and nestling periods. The laying period began with the laying of the first egg and extended until the last egg was laid; the incubation period began with the laying of the last egg and extended until the last egg hatched (in fact, incubation began when the first egg was laid, but for our data presentation and analyses, we defined the incubation period as described here to avoid overlap of data from the laying and incubation periods); the nestling period began with the hatching of the last egg and extended until the last nestling had fledged, or the nest was poached or depredated.

Nest checks.—During the laying and incubation periods, each focal and nonfocal nest was checked daily and its contents inspected; during the nestling period, we reduced the frequency of checks to once per week. On days when a focal nest was the object of behavioral observations, the nest was checked at the conclusion of the observation period, or at least 2 hr before the start of an observation period. This was done to minimize disruption of the adults' behavior. At each nest check, we noted the presence of any new eggs (eggs were numbered with a pencil), used calipers to measure the dimensions (length and width) of new eggs, and noted laying and hatching dates. During the nestling period, we noted morphological characteristics of the hatchlings and the emergence and locations of new feathers, and recorded fledging dates. We also noted evidence of cavity enlargement by the parrots and presence of a nest lining. Although the frequency of nest checks was reduced during the nestling period, we visited nest trees 2 to 3 times per day in order to maintain a presence that, we hoped, would reduce the likelihood that our study nests would be poached.

Poaching interviews.—We obtained information on the techniques used by parrot poachers in the San Juan area through anonymous interviews of individuals actively engaged in the capture and sale of *A. o. panamensis*. Poachers were contacted with the help of an area resident who is familiar with the parrot trade around San Juan. A consistent set of questions or talking points was included in each interview, but the respondents were encouraged to offer any information that they might have regarding the parrots. The interview questions focused on the poaching of *A. o. panamensis*; however, additional information on other species was noted whenever mentioned by the respondents. All interviews were conducted by AMRC.

Statistical analyses.—Descriptive statistics (mean ± SD, range, percentage) are presented for nest site and behavioral data. Data from the 2 years are presented separately in tables, since the 2nd year included data from nests in both partially cleared dry forest and mangrove habitats; however, the descriptive statistics presented in text summarize both years' data. We used the Lilliefors (Kolmogorov-Smirnov) test to check for normality prior to performing parametric tests. We performed chi-square tests of independence to test the hypothesis that parrots prefer cavities in certain tree species. For each habitat, we compared the number of nests (occupied cavities) in different tree species with the number of unoccupied cavities in those species. Chi-square tests of independence were also used to determine whether parrots showed a preference for trees in relatively good condition. We used circular statistics (Batschelet 1981) to analyze the orientation of nest-cavity openings, and performed Rayleigh tests to determine whether the orientations of occupied and unoccupied cavities were random. These tests were performed using R (R Development Core Team 2005); cavity openings facing upward were excluded from the orientation analyses. We performed a discriminant function analysis to determine whether there were significant differences between the dimensions of trees and cavities containing successful nests versus the dimensions of those with nests that were poached or depredated. Discriminant function analysis determines which variables (in our case, nest dimensions) discriminate between two or more groups (successful versus unsuccessful nests), and identifies those variables that contribute most to the differences between groups (Huberty 1994, Silva and Stam 1995). We employed a forward stepwise procedure to select among nine nest dimensions (see Table 1), with entry and removal *P*-values of 0.05. We used linear regression to assess the degree to which time spent by the females in the nest changed through the nestling period. For analyses of data that were not normally distributed, we used Mann-Whitney *U*-tests and Wilcoxon tests. Statistical analyses (with the exception of circular statistics)

TABLE 1. Dimensions of occupied cavities (n = 49) of *Amazona ochrocephala panamensis* in the lowlands of San Juan, Chiriquí, western Panama, 1997–1999.

Measurement	Mean ± SD	Range
Vertical depth (cm)	99.2 ± 71.2	34.8–445.0
Internal width (cm)	26.8 ± 4.3	18.1–34.0
Internal length (cm)	26.8 ± 4.5	16.5–36.0
Area of cavity floor (cm^2)	575.9 ± 175.1	257.3–907.9
Area of cavity entrance (cm^2)	229.7 ± 63.0	149.8–380.1
Horizontal diameter of cavity entrance (cm)	15.6 ± 2.7	10.9–19.8
Vertical diameter of cavity entrance (cm)	17.2 ± 2.8	12.0–22.5
Height of cavity entrance (m)	12.4 ± 2.7	9.2–16.5
Height of nest tree (m)	19.2 ± 3.1	10.7–26.1

were performed using Statistica 6.0 (StatSoft, Inc. 1998). For all tests, statistical significance was set at $\alpha = 0.05$ and means are presented ± SD.

RESULTS

Characterization of nest sites.—In our study area, *A. o. panamensis* used a diversity of tree species for nesting. In mangrove habitat, active nest cavities were found in five tree species: *Rhizophora mangle*, *R. brevistyla*, *Avicennia bicolor*, *Pelliciera rhizophorae*, *Mora oleifera*. In partially cleared dry forest habitat, parrots were found nesting in two species of palms, *Roystonea regia*, *Cocos nucifera*, and in *Ficus insipida* trees. The most frequently used tree species were *R. regia* (18 of 49 nests) and *R. mangle* (13 of 49 nests). The tree species used least frequently were *A. bicolor* and *F. insipida*, each of which was used only once. Overall, parrots showed no preference for nesting cavities in any one tree species in either mangrove or dry forest habitat (mangrove: $\chi^2 = 0.813$, df = 4, $P = 0.94$, $n = 27$ nests; dry forest: $\chi^2 = 0.039$, df = 2, $P = 0.98$, $n = 22$ nests). Rather, the use of tree species for nesting was proportional to cavity availability in those species. We found no evidence in either habitat type that any one tree species is more likely to develop cavities than the others (mangrove: $\chi^2 = 0.257$, df = 4, $P = 0.99$, $n = 41$ cavities; dry forest: $\chi^2 = 0.666$, df = 2, $P = 0.72$, $n = 25$ cavities).

Characteristics of occupied and unoccupied cavities.—Breeding pairs preferred cavities that were relatively high above the ground and with dimensions similar to those reported for other *Amazona* species (see Table 1). The orientation of occupied cavity openings was nonrandom (Rayleigh test: $r = 0.4408$, $P < 0.001$, $n = 39$), with a bias toward the northeast quadrant (25 of 39 occupied nests had orientations between 250° and 360°). In contrast, the orientations of unoccupied cavities were randomly distributed (Rayleigh test; $r = 0.1495$, $P = 0.26$, $n = 61$).

In both habitat types, we found that *A. o. panamensis* preferred trees with single cavities ($\chi^2 = 41.49$, df = 2, $P < 0.001$), possibly because trees with more than one cavity were in poorer condition than those with single cavities. Indeed, parrots preferred trees in relatively good condition. Forty-two of 49 (86%) occupied trees were in good or fair condition, while 56 of 98 (57%) unoccupied trees were in poor condition or they were dead ($\chi^2 = 24.5$, df = 1, $P < 0.001$). Comparing the location of cavities (branch, branch/trunk, or trunk) in occupied versus unoccupied trees indicated that the parrots had no preference for any particular cavity location ($\chi^2 = 0.807$, df = 2, $P = 0.67$).

Pre-laying period.—We observed pairs of *A. o. panamensis* prospecting for nest sites early in each field season (13–30 December 1997, 21 December 1998–5 January 1999). Both members of the breeding pair participated in nest prospecting. On four occasions, we observed one of the two birds apparently take the lead in cautiously approaching and investigating the cavity while its partner remained perched in a nearby tree. Once a nest tree was selected, but before egg-laying began, the female (sex was known for focal pairs once they had been captured and marked) spent long periods of time within the nest cavity, while the male remained perched at the entrance or nearby. On two occasions in the mangrove habitat, a focal female was seen taking a twig into her nest cavity. In a third instance, an individual (sex unknown) took a leafy twig into its nest cavity in a *M. oleifera* tree. Inside 6 of the 49 monitored, occupied cavities, we found wood chips and leaves—materials that were a result of the parrots' chewing activities and/or brought in from outside the cavity.

Throughout the breeding season, pairs often perched together, grooming each other's neck, head, and wings. We observed no copulations or copulation attempts during our study. Prior to the onset of egg-laying, the male occasionally entered the nest cavity with the female and remained inside for several minutes (mean time inside = 3.40 ± 0.44 min, *n* = 17). During these visits, it is likely that he was feeding the female, but it is also possible that copulations occurred. As the egg-laying period approached, the female increased the amount of time that she spent inside the nest cavity, emerging for a few minutes at intervals of 1.5–2.5 hr to stretch her wings and legs before returning to the cavity. During this period, we observed eight instances in which the male presented his mate with flowers of *Erythrina fusca* or *Gliricidia sepium*, which the female subsequently consumed.

Egg-laying and incubation periods.—Egg-laying in the monitored nests (focal and non-focal) occurred from 15 December to 3 January (1997–1998) and 24 December to 13 January (1998–1999). Clutch size averaged 3.08 ± 0.77 eggs over both years of the study (Table 2), with no significant difference between years (Mann-Whitney *U*-test: *Z* = −0.584, *P* = 0.56, *n* = 63 clutches). The mean laying interval was 2.16 ± 0.92 days (Table 2). Incubation began when the first egg was laid and was conducted exclusively by the female. The incubation period lasted 25.14 ± 1.77 days.

During egg-laying and incubation, females spent most of their time inside the nest or perched nearby, and males were never seen entering the nest cavity, although they often remained perched nearby (Fig. 1). The amount of time the male spent with the female during the egg-laying period (the female's fertile period) versus during the incubation period did not differ (Wilcoxon test: *Z* = 1.48, *P* = 0.14, *n* = 10 breeding attempts). During incubation, the female occasionally emerged from the nest

TABLE 2. Breeding parameters of *Amazona ochrocephala panamensis* in the lowlands of San Juan, Chiriquí, western Panama. Data are reported for two breeding seasons: December 1997–April 1998, and December 1998–April 1999.

	1997–1998			1998–1999		
	n	Mean ± SD	Range	*n*	Mean ± SD	Range
Eggs						
Width (mm)	32	28.53 ± 0.74	27.0–30.5	32	28.75 ± 1.05	27.0–30.2
Length (mm)	32	37.45 ± 0.78	36.5–38.2	32	35.96 ± 1.08	33.7–37.5
Clutches						
Clutch size (no. eggs)	21	3.00 ± 0.77	2–4	42	3.12 ± 0.77	2–4
Interval between successive layings (days)	12	2.03 ± 1.06	1–4	9	2.34 ± 0.70	2–5
Duration of incubation (days)	12	25.09 ± 1.91	22–28	9	25.21 ± 1.56	24–29
Interval between successive hatches (days)	12	2.21 ± 1.24	1–5	9	2.13 ± 1.16	1–4
Eggs hatched per clutch	21	2.76 ± 0.77	0–4	42	2.95 ± 0.94	0–4
No. fledged per clutch	21	0.38 ± 1.20	0–4	42	0.48 ± 1.19	0–4
Age at fledging (days)	5	68.60 ± 5.36	59–71	7	78.29 ± 3.88	73–86

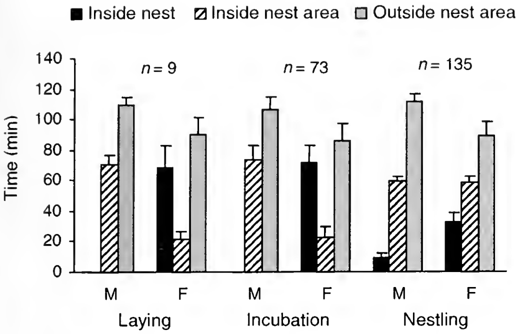

FIG. 1. Mean time (out of 180 min) spent by adult *Amazona ochrocephala panamensis* parrots inside or near the nest, by nesting stage. Data are presented separately for males (M) and females (F); error bars correspond to standard deviations. Sample sizes refer to the number of 3-hr observation periods. The number of pairs observed was as follows: 1997–1998, $n = 5$ during laying, incubation, and nestling stages; 1998–1999, $n = 5$ during laying and incubation stages, and $n = 4$ during the nestling stage. Total observation times were 27, 219, and 405 hr during the laying, incubation, and nestling stages, respectively.

for a short time (8–17 min) to perch at the cavity entrance or on a nearby branch, sometimes engaging in allogrooming with the male. On 10 occasions, the male was observed feeding the female near the nest. Males spent much of their time in the nest area, and typically departed on two foraging trips per day—one in the morning and the other in the late afternoon. Early in the morning and late in the afternoon, the female often left the nest area—possibly to forage with the male (Fig. 1)—and remained out of the nest area for 85.6 ± 11.5 min (range = 61–110 min). For 27 of 83 departures, the pair departed with small groups of two to four other parrots—conspecifics and/or *Amazona autumnalis*. Upon their return, the pairs often flew in the company of other parrots (30 of 83 arrivals). At the end of the day, the male usually departed from the nest area (65% of late afternoon observation periods in 1997–1998, and 76% in 1998–1999), either alone or with other parrots as they passed by. On 11 occasions (involving 10 different nests), we made nocturnal nest checks during the incubation period and examined the nest area with a flashlight; on only three (27%) of the checks did we see the male perched in the nest tree.

Nestling period.—Chicks hatched with their eyes closed, and their bodies were covered with a sparse white down that was later replaced by a gray down, as described by Forshaw (1989). Nestlings spent just over 2 months in their nests before fledging, varying somewhat between the 2 years of the study (mean age at fledging in 1997–1998 = 68.6 ± 5.36 days, $n = 5$ fledglings; mean age at fledging in 1998–1999 = 78.3 ± 3.88 days, $n = 7$ fledglings). Young fledged between 22 March and 5 April in 1998, and between 6 and 24 April in 1999; those hatched during the 1st year fledged in less time than did those hatched during the 2nd year (Mann-Whitney *U*-test: $Z = -2.94$, $n = 12$ fledglings, $P = 0.003$).

We made six nocturnal visits to nests and on five of the visits (83%) the male was found in the nest area, but never inside the nest cavity; in three cases, he was perched near the nest entrance, and twice he was perched a few meters away in a nearby tree. On all six visits, the female was inside the nest (on four of these occasions, the female briefly came to the nest entrance to look out and then quietly went back inside; on the other two visits, she exited the nest and returned ~30 min later).

During the nestling period, we typically found the female inside the nest as we began each observation period (114 of 135 observation periods). She would spend much of her time brooding recently hatched young, but as the nestling period progressed, she decreased the amount of time spent in the nest (linear regression: $F_{1,132} = 419.08$, $P < 0.001$, $R^2 = 0.76$, $b = -2.44$). When outside of the nest, she perched nearby and engaged in allogrooming with her mate and/or she left the nest area, presumably to forage (Fig. 1). Each day during this period, both the male and female would follow their foraging trips with two to four short visits to the nest cavity, presumably to feed the nestlings (males: mean duration = 5.5 ± 1.3 min, range = 2.2–8.3, $n = 135$ observation periods; females: mean duration = 5.1 ± 1.2 min, range = 2.4–7.5, $n = 135$ observation periods).

Nestlings acquired their plumage rather slowly. The flight feathers were the first to appear, with pin feathers for the remiges beginning to emerge when nestlings were 16 to 28 days old. Green contour pin feathers on the wings and yellow contour feathers on the head began to unsheath at 26–30 days, and contour feathers on the legs and back began to unsheath at 35–38 days. At ~40–42 days, the green feathers on the head and red feathers at the bend of the wing began to unsheath. Finally, at ~49–52 days, the tail feathers were completely unsheathed. About 2 weeks before leaving the nest, the nestlings began to perch at the cavity opening. Fledging was asynchronous, and the age at which young left the nest ranged from 59 to 86 days (see Table 2). We observed the nestlings' first flight from the nest on seven occasions; five flights occurred in the morning and two in the late afternoon. The first flights were relatively short (mean distance = 34.6 ± 8.0 m, range = 25.0–48.5, n = 7 fledglings), low, and quiet, and the young were accompanied by one or both adults. After the last chick in a clutch had fledged, neither the young nor the adults entered the nest cavity again; for at least 6 more days, however, the adults continued to visit the nest area. Breeding pairs whose nests were poached by humans or failed due to natural predation did not make a second breeding attempt in the same cavity that year; however, they continued to visit the nest area for at least 6 days following nest failure.

Breeding success.—We obtained productivity data for 63 breeding attempts (Table 2). Overall, breeding success of *A. o. panamensis* was very low. Over both breeding seasons, only 12.7% (8 of 63) of nests fledged young. Of the remaining nests, 9.5% (6 of 63) failed due to natural predation at the nestling stage, all of which we visually confirmed as predation by boas (*Boa constrictor*). The principal cause of breeding failure was nest poaching by humans. A total of 77.8% of nests (49 of 63) were poached or presumed to have been poached. Poachers accessed nest contents by chopping holes in trunks at the level of the nest cavity (17 of 49 poached nests), climbing trees to reach nests (27 of 49), and less frequently by felling trees (5 of 49). The disappearance of nestlings often coincided with evidence of machete cutting of understory vegetation near the nest tree (17 of 49 poached nests).

Fourteen of the 19 cavities (74%) containing nests that failed due to predation or poaching during the 1st year were reused during the following breeding season. Only 8 of 49 cavities monitored during one or both breeding seasons housed nests that successfully fledged young, but we found no evidence of a relationship between breeding success and the dimensions of nest trees or nest cavities. Discriminant function analysis indicated that the dimensions of trees and cavities containing successful versus failed (poached or depredated) nests did not differ (Wilks' Lambda = 0.7468, $F_{9,39} = 1.47$, $P = 0.19$, $n = 49$ nests); only cavity depth contributed significantly to the discriminant function (Wilks' Lambda = 0.8953, $P = 0.008$).

Poaching techniques and illegal trade.—Eighteen parrot poachers were interviewed, and they described a range of poaching strategies that included the removal of unhatched eggs, newly hatched nestlings, fully feathered nestlings, and the capture of recently fledged juveniles. The majority of poachers (13 of 18) preferred fully feathered nestlings ~40 days old and only one of the poachers took newly hatched young (3 to 8 days old). Relatively few poachers (2 of 18) took eggs from the nest, and the remainder (2 of 18) preferred to capture juveniles that had already fledged. None of the poachers targeted adult parrots.

More than three quarters of the poachers (14 of 18) considered the demand for *A. o. panamensis* nestlings to be very high, and said that they always had customers lined up to purchase birds even before they had been taken from their nests. Many of the poached birds are sold locally to customers in Chiriquí, but poachers indicated that vacationers from Panama City and truck drivers involved in the transport of merchandise between Panama and Costa Rica pay the highest prices (as much as US$100 for a fully feathered and healthy parrot chick). Half of the poachers said that they typically sold parrot nestlings for $40 or more; most of the others (8 of 18, 44.4%) sold nestlings for $30–39, and only one of the poachers sold nestlings for $20–29. Poachers were not asked to reveal total annual earnings from poaching, but five volunteered this information: four indicated that they typically made $200–350 per year and one said that he never earned less than $200 annually and sometimes made as much as $750 per year. For comparison, the typical monthly salary for a farm laborer in the area is $130. According to a 1990 census (Dirección General de Estadística y

Censo de Panamá 1991), the human population in the study area was approximately 2,358, but the number of people involved in poaching activities is difficult to estimate. Poaching of parrot nestlings is punishable by fines of up to $1,000, but poachers indicated that if they were caught, the authorities typically seized the nestlings and did not impose any further punishment.

Fifteen of the poachers interviewed (83%) said that they usually collected 6–9 nestlings per breeding season, and the remaining individuals typically collected 2–5 nestlings per season. Most of the poachers (13 of 18) said that they have been collecting and selling parrot nestlings for 7–13 years, and the others have done so for 1–6 years. Eleven poachers (61%) noted that, in the past, they had also taken *A. autumnalis* nestlings, but no longer did so because this species is not a good imitator of human speech and therefore is much less marketable than *A. o. panamensis*. Eight poachers said that both of these species were hunted for food in eastern Chiriquí, but five of the men indicated that this practice is no longer common, especially in the case of *A. o. panamensis*, which could be sold for a relatively high price. Recently, some poachers have begun to use yellow dye on the forehead feathers of *A. autumnalis* and even *Aratinga pertinax* (both of which are less desirable than *A. ochrocephala* in the pet trade), in order to sell them to unsuspecting buyers as *A. ochrocephala* (AMRC pers. obs.). These data indicate that poaching of *A. o. panamensis* is not a new phenomenon and has likely impacted resident populations of the species by reducing recruitment of juveniles.

DISCUSSION

Characterization of nesting habitats and cavities used for breeding.—Breeding pairs of *A. o. panamensis* preferred relatively large cavities high up in trees and palms. The dimensions of the cavities used by these parrots was within the range of those reported for other *Amazona* species, such as *A. vittata* (Snyder et al. 1987), *A. leucocephala bahamensis* (Gnam 1991) and *A. barbadensis* (Rojas-Suárez 1994).

We found no evidence that *A. o. panamensis* prefers to nest in any one species of tree; the frequency of nests in different tree species reflected the frequency of cavity occurrence in those species. Saunders (1979) found a similar lack of preference in a study of *Calyptorhynchus baudinii latirostris*; in three of four nesting areas studied, the dominant tree species housed the majority of nests. Snyder et al. (1987) found that most *A. vittata* nests are in palo colorado (*Cyrilla racemiflora*), but this was due to the scarcity of cavities in other tree species found in the parrots' habitat. In our study, breeding pairs preferred trees in good or fair condition. This contrasts with the finding of Sauad et al. (1991), who found that 72% of *A. aestiva* nests were in trees that were in poor condition or dead. Similarly, *Calyptorhynchus magnificus* tended to nest in dead trees more often than expected by chance (Saunders et al. 1982).

In our study area in western Panama, we found that openings of cavities occupied by breeding *A. o. panamensis* tended to be oriented toward the northeast. A similar preference for certain orientations has been documented for several other parrots (Rodríguez-Vidal 1959, Saunders 1979; but see Saunders et al. 1982, Sauad et al. 1991).

Breeding behavior.—The breeding behavior of *A. o. panamensis* is similar to that reported for other psittacids. Pairs are socially monogamous and both members of the pair contribute significantly to nest defense and caring of young. Allofeeding of the female by her mate, which we observed on several occasions, is typical of breeding parrots (Skeate 1984, Snyder et al. 1987, Gnam 1991, Eberhard 1998), especially early in the breeding cycle (Snyder et al. 1987, Eberhard 1998). Nevertheless, female *A. o. panamensis* did not appear to depend on their mates for food; they regularly left the nest area with their mates, presumably to forage.

Females typically laid eggs at 2-day intervals, as reported for other congeners (*A. vittata*, Snyder et al. 1987; *A. leucocephala bahamensis*, Gnam 1991; and *A. barbadensis*, Rojas-Suárez 1994), though they occasionally laid eggs on successive days or at intervals of up to 5 days. Clutch size varied from two to four eggs, as reported for *A. vittata* (Snyder et al. 1987), and the duration of incubation was similar to that reported for other *Amazona* parrots (Low 1972, Skeate 1984, Snyder et al. 1987, and Rojas-Suárez 1994). As in many other parrots (Forshaw 1989), incubation began when the first egg was laid, resulting in asynchronous hatching, and the female was responsible for incubation. During incubation, the female occasionally emerged from the nest for a few minutes at a time to stretch, groom, and participate in nest defense; in the early morning and late afternoon she often departed for longer times, possibly to forage. The substantial proportion of time spent outside of the nest during this period was greater than that reported for other *Amazona* parrots (e.g., Snyder et al. 1987, Wilson et al. 1995, Renton and Salinas-Melgoza 1999). In *A. vittata*, low nest attendance and long recesses by female parrots were associated with failed nesting attempts (Wilson et al. 1997); we observed similar behaviors in *A. o. panamensis*, but they did not appear to negatively impact breeding success, and the duration of incubation and the number of eggs hatched per clutch in our study were similar to those reported for other *Amazona* parrots (Low 1972, Snyder et al. 1987, Gnam 1991, Rojas-Suárez 1994). The long departures by *A. o. panamensis* females might be due to habitat fragmentation in our study area, which in turn has disrupted the parrots' foraging patterns, as observed by Saunders (1990) in a study of Carnaby's Cockatoo (*Calyptorhynchus funereus latirostris*) in agricultural areas.

During incubation, we never saw the male enter the nest; this contrasts with observations of *A. albifrons* (Skeate 1984) and *A. vittata* (Snyder et al. 1987), in which males occasionally enter the nest during this period. In *A. o. panamensis*, the male spent much of his time near the nest while his mate was incubating, possibly to alert her to approaching predators or prevent extra-pair copulations by his mate with other males; however, the time the male spent in the nest area did not differ between the egg-laying (when the female is fertile) and incubation periods, suggesting that he was not mate-guarding.

The female was apparently responsible for feeding the newly hatched chicks, but a few days after the eggs had hatched, the male began to enter the nest regularly, presumably to feed the young. This also has been reported for other *Amazona* parrots, including *A. albifrons* (Skeate 1984), *A. l. bahamensis* (Gnam 1991), and *A. vittata* (Snyder et al. 1987, Wilson et al. 1995). As the nestlings grew, the female gradually reduced the amount of time she spent in the nest with them. She ceased brooding the young during the day when the oldest nestling was 18 to 25 days old, similar to that observed in other *Amazona* species (e.g., Snyder et al. 1987, Enkerlin-Hoeflich and Hogan 1997, Renton and Salinas-Melgoza 1999).

Chicks of a single clutch usually fledged on different days, as reported for *A. vittata* (Snyder et al. 1987) and *A. l. bahamensis* (Gnam 1991). Mean age at fledging was greater than that reported by Snyder et al. (1987) for *A. vittata*, by Rojas-Suárez (1994) for *A. barbadensis*, and by Renton and Salinas-Melgoza (1999) for *A. finschi*. As described for *A. l. bahamensis* (Gnam 1991), fledglings were accompanied by one or both parents on their first flight, but the flights of *A. o. panamensis* fledglings were shorter. After leaving the nest, *A. o. panamensis* fledglings were very quiet, probably to avoid attracting the attention of predators; similar cryptic behavior has been observed in *A. vittata* (Snyder et al. 1987).

Breeding success.—In our study area, the breeding success of *A. o. panamensis* was low, principally due to poaching, and to a lesser extent to natural predation by boas. Habitat loss due to deforestation, which often involves felling of the largest trees, has been cited as an important cause of population declines among parrots (Juniper and Parr 1998). However, in the case of *A. o. panamensis* in western Panama, our results indicate that breeding is not limited by the availability of nesting sites, even though much of the area has been partially cleared. The very low rate of breeding success is instead due to extremely high poaching rates fueled by demands of the local pet trade. Low salaries and the lack of employment opportunities in the San Juan area undoubtedly drive individuals to poach parrot nestlings. Although the activity is illegal and punishable by fines of up to $1,000, anti-poaching laws are only weakly enforced. Because favored poaching techniques are focused on collecting nestlings, recruitment into the *A. o. panamensis* population is severely reduced, and the population is in danger of a rapid and precipitous decline as the adults age and are not replaced by individuals from younger age classes.

ACKNOWLEDGMENTS

We thank the owners and laborers of Hacienda El Tekal, Hacienda Miraflores, and Hacienda Los Asentamientos de San Juan for their collaboration and for allowing access to their properties. Partial financial support was provided by the German Technical Cooperation Agency through its Proyecto Agroforestal Ngöbe-ANAM-GTZ. We are grateful that some of the parrot poachers were willing to reveal information about their activities, which may help in developing future conservation measures. We also thank the residents of the Corregimiento de San Juan, especially those engaged in the collection and sale of parrots in the local pet trade, for sharing information on their poaching activities. Two poachers were helpful in locating nests as well as establishing contacts with poachers and others involved in the local parrot trade. We thank K. Harms for assistance with performing statistical tests in R, and F. Gómez and E. de Morris for their comments on an early version of the manuscript; the manuscript also benefited from extensive comments provided by three anonymous reviewers.

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The Wilson Journal of Ornithology 118(2):237–243, 2006

GREGARIOUS NESTING BEHAVIOR OF THICK-BILLED PARROTS (*RHYNCHOPSITTA PACHYRHYNCHA*) IN ASPEN STANDS

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ABSTRACT.—We studied Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) nest-site density and social nesting behavior from 1998 to 2001 in Madera, Chihuahua, Mexico. The species formed high-density nesting clusters; 45 nesting attempts (30%) involved nesting pairs sharing nest trees, with a maximum of three nesting pairs per tree. The majority of nest trees were live or dead quaking aspens (*Populus tremuloides*). Clusters contained a mean of 11.5 breeding pairs (5 nests/ha). The highly social nesting behavior of Thick-billed Parrots may have important implications for management and conservation of their breeding habitat. *Received 31 March 2005, accepted 8 January 2006.*

Approximately 13% of all bird species nest in colonies (Gill 1990). Colonial or gregarious nesting behavior provides important advantages for birds, including mate access, reduced probability of nest predation, improved detection and defense against aerial predators while feeding, and enhanced foraging efficiency (Siegel-Causey and Kharitonov 1990, Danchin and Wagner 1997, Eberhard 2002). Despite the advantages of colonial nesting, nest-site availability may be a limiting factor for social species, especially those that nest in tree cavities (Eberhard 2002).

Colonial nesting is uncommon in tree-cavity nesting species and it is particularly rare among Neotropical parrots for two reasons: (1) closely spaced tree cavities with suitable characteristics for nesting are rare, and (2) most parrot species are territorial around nest sites (Forshaw 1989, Munn 1992, Iñigo-Elias 1996). Of the 231 parrot species, Eberhard (2002) reported that only 3 breed colonially.

In Mexico, 20 parrot species nest in tree cavities, 4 of which (genus *Aratinga*) also nest in termitaries (Hardy 1963, Forshaw 1989, Howell and Webb 1995, Rodríguez-Estrella et al. 1995). Both Maroon-fronted Parrots (*Rhynchopsitta terrisi*) and Military Macaws (*Ara militaris*) sometimes nest at high densities in cliff crevices, thus forming nesting colonies (Forshaw 1989, Macías-Caballero 1998). Prior to our study, cavity-nesting parrot species in Mexico were not thought to nest colonially in tree cavities, nor had there been reports of multiple pairs nesting within the same tree (Enkerlin-Hoeflich 1995, Renton and Salinas-Melgoza 1999). Although most parrots are social and have been considered "suppressed colonial breeders" (Ward and Zahavi 1973), the relative density of suitable tree cavities is low and competition for cavities is high (Munn 1992, Gibbs et al. 1993).

The Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) is a highly social species that breeds at elevations from 2,000 to 2,700 m in mature and old-growth coniferous forests in the northern portions of the Sierra Madre Occidental, northwestern Mexico. Social behaviors include the formation of foraging flocks, sentinel posting during foraging, simultaneous courtship and copulations of several pairs in neighboring trees, loud vocalizations of neighboring nesting pairs, synchronized defense against raptors, and the formation of large, nomadic flocks in winter (Lanning and Shiflett 1983; Snyder et al. 1994, 1999). Even when distances among nests are substantial, males of neighboring nesting pairs communicate and wait for each other when forming foraging flocks (Snyder et al. 1999, Monterrubio-Rico and Enkerlin-Hoeflich 2004b).

After decades of intensive logging, few large fragments of old-growth forest remain in the Sierra Madre Occidental; thus, the number

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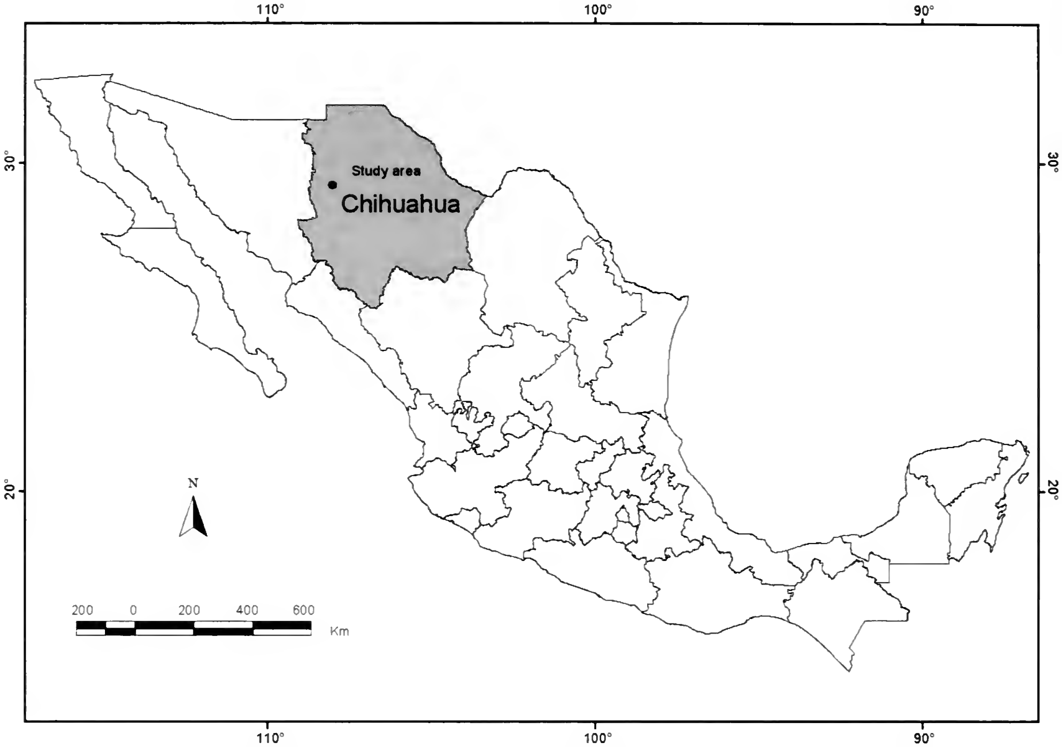

FIG. 1. Thick-billed Parrot study area near Madera, Chihuahua, Mexico, 1998–2001.

and quality of Thick-billed Parrot nesting areas has been reduced and the availability of food resources has probably been altered (Lanning and Shiflett 1983, Benkman 1993, Lammertink et al. 1996). Only five nesting areas are known to remain in the species' breeding range, and two of them (Cebadillas de Yahuirachi and Madera) encompass >70% of the known nesting trees (Monterrubio-Rico and Enkerlin-Hoeflich 2004a). Our objectives were to evaluate nest-site use, nest-tree distribution, density of nesting pairs, and tree sharing by nesting pairs.

METHODS

The study area was near Madera, Chihuahua, at the eastern edge of the Sierra Madre Occidental, (29° 19′ N, 108° 11′ W; Fig. 1). Common tree species included Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), Mexican white pine (*Pinus ayacahuite*), and quaking aspen (*Populus tremuloides*). We monitored breeding activity from July to late October in 1998–2001. The total area surveyed for nests increased each year from 5 ha in 1998 to 75 ha in 2001. Because time, personnel, and access to nesting areas were limited, however, we were unable to completely sample and map the distributions of aspen stands and nest trees.

We found nests by conducting intensive searches during the prospecting and courtship phases of the nesting cycle. A tree cavity was considered a potential nest site if a nesting pair was observed entering the cavity during the egg-laying period (late July). When possible, we used climbing equipment to confirm presence of eggs or nestlings; inaccessible tree cavities were confirmed as nesting cavities when nestlings could be heard or adult parrots were observed feeding nestlings. A tree cavity was considered a roost site if it was used by the parrots but never contained eggs. Because nesting parrots were not individually marked, it is likely that some birds were sampled in multiple years; thus, we report our results in terms of nesting attempts rather than number of pairs.

For each nest tree, we documented species, condition (live or dead), diameter at breast

TABLE 1. Use of nest and roost trees by Thick-billed Parrots, Madera, Chihuahua, Mexico, 1998–2001.

Parameter	Number per year				
	1998	1999	2000	2001	1998–2001
Nesting pairs (attempts)	20	24	30	73	147
Nest trees	17	23	28	55	123[a]
Nest trees used by one pair	14	22	26	40	102
Nest trees with >1 pair	3	1	2	15	21
Nesting pairs sharing a tree	6	2	4	33	45
Trees used as roost sites	3	3	9	15	30

[a] 72 different nest trees: 40 used once, 18 used twice, 9 used three times, 5 used four times = 123.

height (dbh), cavity height, and tree height. The coordinates of each nest tree were obtained with a Geographic Positioning System (GPS), and locations were plotted on topographic maps (scale 1:50,000). Distances between neighboring nesting trees were measured with a 50-m tape or determined from GPS coordinates (for trees >100 m apart). Nest-tree distribution was analyzed with Geographic Information System software (GIS; Arc View 3.3) using geographic coordinates with six decimals. GIS was also used to generate a map and analyze nest distribution.

We defined a "colony" as an aggregation of interacting neighboring groups of nesting pairs. We used the minimum convex polygon criterion to define nesting clusters, where a cluster consisted of ≥3 nests, each ≤150 m from any other nest; the significance level was set at $\alpha = 0.05$ and means are presented ± SD. Statistical analyses were performed with SAS (SAS Institute, Inc. 1985).

RESULTS

During 4 years of study, we documented 147 nesting attempts in 72 different trees; we also documented 10 different trees used as roost sites. We monitored 48 of the nest trees for at least 2 nesting seasons and found that 33 (68%) were reused in subsequent years; mean annual reuse was 62 ± 0.08% (range = 56–71%). Eighty of the 82 trees used for nesting or roosting were aspen, and 2 were Mexican white pine. Aspen snags ($n = 39$) and live aspen ($n = 41$) were used with similar frequency, and 25% ($n = 18$) of the snags were severely deteriorated (total absence of bark). The majority of all 147 nesting attempts (86%) occurred in tree cavities that appeared to be old woodpecker holes, but 20 nesting attempts (14%) occurred in natural cavities formed by tree decay and detachment of large branches. We also recorded 30 cavities used as roost sites (Table 1).

Sixty-nine percent (102) of the nesting attempts involved only one pair of parrots per nest tree. The 45 remaining attempts (30%), however, involved more than one pair per tree: 18 attempts involved two nesting pairs using different cavities in the same nest tree, and three times we observed three nesting pairs sharing different cavities in the same tree (Table 1). We found more nesting pairs in 2001 ($n = 73$) than in other years (Table 1), but that was also the year in which the greatest area (75 ha) was searched for nests.

Overall, the parameters of trees containing multiple cavities did not differ significantly from those containing only one cavity. Nest trees containing >1 active nest did not differ in dbh (Wilcoxon $Z = 0.38$, $P = 0.70$; multiple-nest trees: 57.0 ± 12.2 cm; single-nest trees: 57.8 ± 11.9 cm) or tree height (Wilcoxon $Z = 1.82$; $P = 0.068$; multiple nest trees: 28.0 ± 5.4 m; single nest trees: 24.7 ± 6.0 m). Vertical distance between nest cavities in multiple-nest trees ranged from 1 to 11 m (mean = 4.3 ± 2.9 m). Nest-cavity height ranged from 6.5 to 31 m above ground in single-nest trees and from 9 to 21 m (lowest cavity) in multiple-nest trees.

Most nest trees used by Thick-billed Parrots showed a clumped distribution pattern, forming aggregations (nest clusters) in aspen stands (Fig. 2). Mean nest cluster area was 2.3 ± 1.7 ha, (range = 0.04–4.4 ha), and mean within-cluster nest density was 20.9 ± 32.6 per ha (range = 2.4–100 nests/ha; Table 2). Mean within-cluster distance between active nests was 31.9 ± 26.4 m (range = 1.8–146 m, $n = 147$), and mean distance between clus-

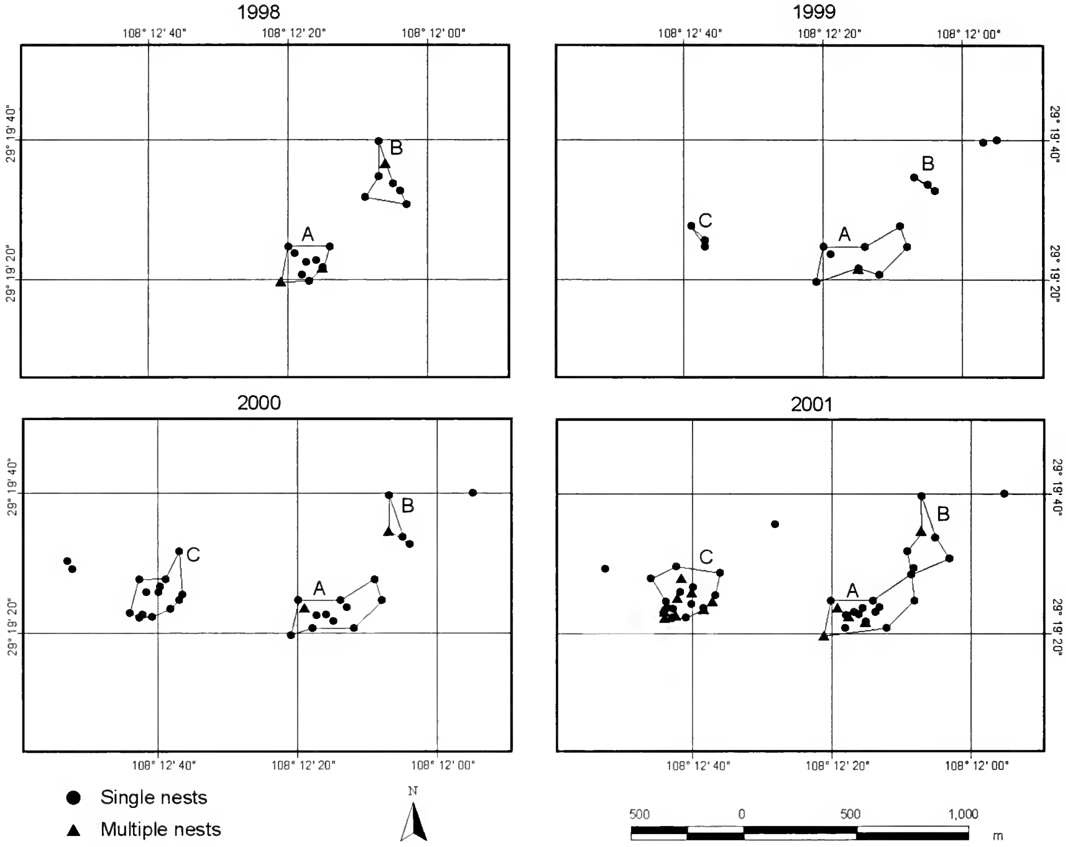

FIG. 2. Diagram showing the distribution of nesting trees, by year, in 11 Thick-billed Parrot nesting clusters in Madera, Chihuahua, Mexico. Nesting clusters were defined using the minimum convex polygon criterion. Capital letters indicate the different clusters, filled circles represent nest trees with one nest, and triangles represent nest trees with two or three nests.

ters was 325 ± 125 m (range = 185–458 m, n = 11). The mean number of nesting attempts per cluster was 11.5 ± 8.1 (range = 3–31).

No agonistic behavior was observed among nesting pairs. Neighboring nesting pairs were in permanent contact: synchronized foraging flocks formed every morning and communication among pairs occurred with loud vocalizations and visual contact. We also observed five events of collective responses to raptors, in which parrots rapidly formed a flock after sharp alarm calls had been emitted by the parrots that first detected the raptors.

DISCUSSION

Nest site density.—The Thick-billed Parrot is a social species that tolerates other nesting pairs, often in the same nest tree. Previously, Lanning and Shiflett (1983) had observed two active nests (only 2 m apart) in a pine snag. They also observed two pairs nesting in a large aspen within 215 m of three other nests and within 1 km of six additional nests. However, we observed considerably greater nest density and number of nesting pairs sharing nest trees than those reported by Lanning and Shiflett (1983) and Snyder et al. (1999). The mean distance between active nests (31.9 m) and the shortest distance (1.8 m) between nesting pairs of Thick-billed Parrots were the smallest values reported for any cavity-nesting parrot species in Mexico. For example, the same values for Lilac-crowned Parrot (*Amazona finschi*) in the tropical subdeciduous forests of the Chamela-Cuixmala Biosphere Reserve were 948 m and 25 m, respectively (Renton and Salinas-Melgoza 1999). The

TABLE 2. Characteristics of Thick-billed Parrot nest clusters in aspen stands, Madera, Chihuahua, Mexico, 1998–2001.

Parameter	1998	1999	2000	2001	1998–2001
No. of clusters	2	3	3	3	11
Mean no. of nests/cluster (range)	10.0 (8–12)	5.3 (3–10)	10.3 (5–13)	19.6 (8–31)	11.5 (3–31)
Mean size (ha) of nesting clusters (range)	1.9 (1.4–2.2)	1.4 (0.04–4.1)	2.5 (0.05–4.4)	3.1 (2.2–4.2)	2.3 (0.04–4.4)
Mean nest density/ha in clusters (range)	5.4 (5.4–5.5)	36.8 (2.4–75.0)	35.6 (3.0–100.0)	5.8 (3.5–7.3)	20.9 (2.4–100.0)

clumped nest distribution and multiple nests per tree of Thick-billed Parrots observed in Madera may be explained by (1) the existence of adequate tree cavities at high densities and (2) the species' high level of sociality and tolerance of neighboring nesting pairs. It also may be that nesting pairs experience lower rates of predation by selecting tree cavities near other pairs.

Conservation and management recommendations.—In addition to high nest density, we also documented >50% reuse of cavities by Thick-billed Parrots. Lanning and Shiflett (1983) recorded lower nest densities and a lower level of cavity reuse (1 of 12 nesting cavities in good condition were reused). High nest density and reuse of cavities may indicate a scarcity of adequate nesting cavities in the surrounding conifer forests. Several authors have addressed the alarming reduction in the extent of old-growth conifer forests in the Sierra Madre Occidental and its negative impact on the Thick-billed Parrot (Lanning and Shiflett 1983, Lammertink et al. 1996, Snyder et al. 1999). As a result of habitat loss, most of the nesting activity is now concentrated in two areas (Cebadillas de Yahuirachi and Madera), making the species vulnerable to the effects of illegal logging, forest fires, and conifer crop failures (Benkman 1993, Snyder et al. 1994, Monterrubio-Rico and Enkerlin-Hoeflich 2004a).

A fundamental conservation goal for Thick-billed Parrots should be to increase the number of nesting areas. This can be achieved by protecting stands of old-growth in all current and historical nesting areas, especially those in the high-elevation (2,000–3,000 m) forests of Durango and Chihuahua. Because trees large enough to support suitable cavities may take 4 decades or more to form, nest boxes should be erected to augment nest-site availability. Although it remains unknown whether Thick-billed Parrots will use nest boxes in the wild, they are known to use them in captivity (Snyder et al. 1994). Retaining old-growth coniferous forest will also ensure seed availability (Benkman 1993) and nesting opportunities for other obligate cavity nesters, such as Eared Quetzal (*Euptilotis neoxenus*), and Mexican Spotted Owl (*Strix occidentalis lucida*)—species that nest in the same habitats as Thick-billed Parrot.

Areas managed for Thick-billed Parrots should include tree species commonly used as nest sites, such as Mexican white pine, Douglas-fir, and aspen. In addition, pine species such as Durango pine (*Pinus durangensis*), teocote pine (*Pinus teocote*), Chihuahuan pine (*Pinus leiophylla*), and Apache pine (*Pinus engelmannii*), should be included to provide a constant cone crop (Snyder et al. 1999). Although stands of large aspen are uncommon in conifer forests of the Sierra Madre Occidental, aspens can be planted in more humid areas selected for restoration.

Populations of Thick-billed Parrots are relatively small, even in the most important nesting areas. Thus, the species' recovery will require sustained periods of high nesting success and productivity. This can be achieved only by providing parrot populations with adequate nesting opportunities across the landscape.

ACKNOWLEDGMENTS

We appreciate the help and advice of N. F. R. Snyder, R. B. Hamilton, K. Renton, M. S. Hafner, C. Macias, M. A. Cruz-Nieto, C. Valle, and J. Shiflett. Financial support was provided by CONABIO (Mexico Biodiversity Commission), Sacramento Zoo, National Fish and Wildlife Foundation, Arizona Game and Fish Department, USFWS/SEMARNAT program in Biodiversity Conservation for NAFTA initiative, Wildlife Preservation Trust, Fondo Sectorial Ambiental SEMARNAT-CONACYT, Centro de Calidad Ambiental at Instituto Tecnológico y Estudios Superiores de Monterrey, and the School of Renewable Natural Resources at Louisiana State University. We thank the Coordinación de Investigación Científica and Facultad de Biología at Universidad Michoacana de San Nicolás de Hidalgo for their continued logistical and economic support, and the Dirección General de Vida Silvestre at SEMARNAT, which provided research authorizations. We also thank J. W. Wiley and two anonymous reviewers who made important suggestions that improved this manuscript.

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Short Communications

The Wilson Journal of Ornithology 118(2):244–247, 2006

No Extra-pair Fertilization Observed in Nazca Booby (*Sula granti*) Broods

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ABSTRACT.—Nazca Booby (*Sula granti*) broods in the Galapagos Islands showed 0% extra-pair fertilization, based on multilocus band-sharing values. The 95% CI of this estimate for all chicks was 0–0.098, and for all broods it was 0–0.139. These are the first data on extra-pair paternity to be reported for a member of the family Sulidae. *Received 6 September 2005, accepted 22 February 2006.*

The frequency of extra-pair paternity (EPP) among bird species varies widely, from 0% in some seabirds (e.g., Chinstrap Penguins, *Pygoscelis antarctica*; Moreno et al. 2000), the Acorn Woodpecker (*Melanerpes formicivorus*; Dickinson et al. 1995, Haydock et al. 2001), and other taxa (Griffith et al. 2002) to 72% in Superb Fairy-wrens (*Malurus cyaneus*; Mulder et al. 1994, Double and Cockburn 2000). Application of new molecular genetic techniques has enabled the recent explosion in availability of parentage data from birds, and estimates of EPP exist for at least 186 species in at least 39 families (Griffith et al. 2002, Spottiswoode and Møller 2004). Of particular interest is the minority (25%) of socially monogamous taxa in which EPP is absent, or nearly so (Griffith et al. 2002). In departing from the general trend in birds, these taxa may experience selection pressures, or phylogenetic constraints, that differ from those of most species, and they can provide insight into the evolution of the vast diversity of mating systems in birds. The majority of the diversity in EPP frequency is at or above the family level in birds (Arnold and Owens 2002); thus, comparative analyses (Bennett and Owens 2002, Westneat and Stewart 2003) require data from as many higher-order taxa as possible.

Here, we present parentage data from Nazca Boobies (*Sula granti*), a socially monogamous seabird in the family Sulidae, for which published data on EPP frequency is lacking. While Nazca Boobies exhibit life-history characteristics associated with a low EPP rate (Bennett and Owens 2002)—such as long life, extended parental care, and small broods (Anderson 1993, Anderson and Apanius 2003)—they nest colonially in the presence of many potential copulatory partners (Nelson 1978), females spend extended periods unattended in the colony while their mate forages at sea, and they have unusually low hatching success (60%) due to infertility or early embryo death (Anderson 1990). The low hatching success could be due to low sperm quality in some males, which might induce females to select for insurance sperm outside the pair bond, although other aspects of their life history suggest that EPP should be rare.

In 1990, we studied Nazca Boobies breeding at the large colony at Punta Cevallos, Isla Española, Galapagos Islands, Ecuador (1° 20′ S, 89° 40′ W). Huyvaert and Anderson (2004) give details of the study site. We collected blood samples from 10 single-chick broods (January 1990, with unknown initial clutch and brood sizes) and 13 two-chick broods (December 1990) and their social parents (adults that brooded the young). In this population, clutch size is either one or two (Anderson 1990); hence, the December sample almost certainly represents complete families, but we are not certain about initial clutch or brood size of the January sample. Single-chick broods in the first sampling effort were the products of single chicks from one- or two-egg clutches, or the survivor of obligate siblicide (almost always the first-hatched

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chick) in a two-chick brood (Humphries et al. 2006). Two-chick broods were targeted in the second sampling effort to determine whether siblicide masked a high EPP rate in second-hatched chicks. Families were chosen randomly from across the colony and had typical distances to neighboring sites (mean = 2.7 m ± 1.55 SD; Anderson 1993). Using syringes, we drew blood samples from the brachial vein and transferred them to vacutainers. Blood was stored in Queens lysis buffer (Seutin et al. 1991) at ambient temperature in the field and later at 4° C. DNA was extracted from the blood samples following the procedures of Seutin et al. (1991). After testing various combinations of restriction enzymes and multilocus probes for quality and quantity of bands, all booby DNA was cut with *Mbo I* and hybridized with radioactively labeled minisatellite probes 33.15 (Jeffreys et al. 1985) and *per* (Shin et al. 1985). Electrophoresis, Southern blotting, and prehybridization followed Smith et al. (1991), except that we used 5 μg of DNA per sample, and Immobilon (Millipore) transfer membranes. Transfer membranes were hybridized, washed, and autoradiographed following Smith et al. (1991), except that the membranes were washed in 2× SSC, 0.1% SDS. After probing with both minisatellites, the membranes were probed a third time with lambda DNA to reveal lambda size markers in each lane to facilitate scoring of homologous fragments in different lanes.

We assessed parentage of nestlings by comparing bands in the 2- to 12-kb range of nestlings with those of their putative parents on the autoradiographs. Bands were scored by marking acetate sheets, using different colors for maternally and paternally derived bands. Bands were considered identical if their centers were less than 1 mm apart and they did not differ greatly in density. We calculated the degree of band-sharing between putative parents and offspring to determine whether we could exclude a parent and, if so, which one. Band-sharing (D) was calculated as $D = 2\ (n_{AB})/(n_A + n_B)$, where n_{AB} is the number of bands shared by birds A and B, and n_A and n_B are the number of bands in birds A and B, respectively (Wetton et al. 1987). Both Jeffreys 33.15 and *per* probes produced DNA fingerprints similar to those described for other bird species. Band-sharing was calculated as the mean of the D values of the two probes. We used the band-sharing of mates as an estimate of the band-sharing of unrelated birds, and used that estimate to evaluate the relationship of putative parents and their offspring. Because the probability of a brood having two chicks increased with increasing band-sharing values (logistic regression, $\chi^2 = 4.34$, df = 1, $P = 0.037$), we evaluated the January 1990 and December 1990 groups separately; generally, band-sharing was greater in the December sample, for all pairwise analyses of family members. Because there was no *a priori* difference in how families were selected in the two sampling periods, and given that the two sets of DNA fingerprints were prepared by different lab workers at different times, the difference in average similarity values may have resulted from methodological differences, not biological differences in relatedness.

In one-chick broods, band-sharing of mated pairs averaged 0.330 ± 0.115 SD; band-sharing between offspring and mothers averaged 0.617 ± 0.076 and that between offspring and fathers averaged 0.625 ± 0.066. The smallest band-sharing value between an offspring and a parent (0.533) exceeded the largest value of band-sharing in mated pairs (0.527; Fig. 1). These non-overlapping distributions provide no indication of extra-pair parentage in one-chick broods.

In two-chick broods, band-sharing of mated pairs averaged 0.418 ± 0.106; band-sharing between offspring and mothers averaged 0.699 ± 0.073, and between offspring and fathers it averaged 0.680 ± 0.117. Although four band-sharing values between an offspring and a parent were less than the largest value of band-sharing in mated pairs (0.564; Fig. 1), they do not provide reliable evidence of extra-pair parentage. In three cases (indicated by parentheses in Fig. 1), DNA degradation in parental samples caused low band-sharing values between all members of the family, including between the mated adults. The offspring in this family displayed no unattributable bands, indicating that the putative parents were in fact the genetic parents. This was the lone instance of poor quality DNA among our samples. In the remaining two cases (indicated by the rotated parentheses in Fig. 1), the identity of the social father was questioned on behavioral grounds after blood samples

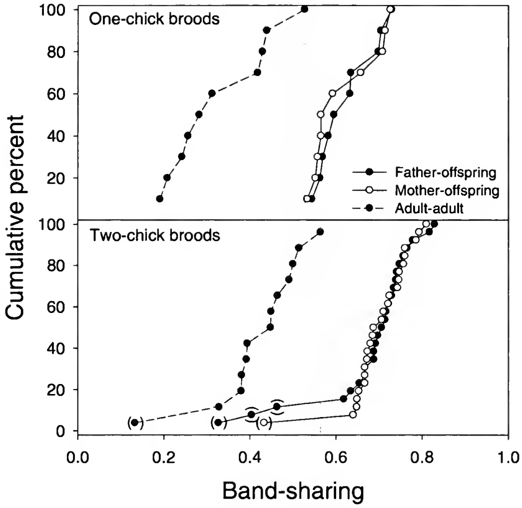

FIG. 1. Distribution of band-sharing values in Nazca Booby broods, expressed as cumulative percentages from lowest to highest values. Dotted vertical lines show the maximum band-sharing value for unrelated adults (mated pairs). Values in parentheses are the result of either poor quality DNA (●) or uncertain parentage $\overset{\frown}{\bullet}$. Blood samples were collected in January and December 1990 at Punta Cevallos, Isla Española, Galapagos, Ecuador.

had been taken from the two offspring and two adults present at the nest site. At the time of sampling, we had observed a male standing near the female and offspring, and assumed that he was the social father; on subsequent days, however, another male consistently attended this brood and the original male instead appeared to be a neighbor. We were not able to obtain a blood sample from the other putative father. This was the one instance in which family membership was uncertain. Omitting these two families from consideration, all band-sharing values of offspring and putative parents exceeded the largest band-sharing value of mated adults in two-chick broods (0.564; Fig. 1). Excluding the four chicks of the two questionable broods, our estimate of EPP frequency in the 32 chicks was 0 (95% CI = 0–0.109), and in the 21 broods it was also 0 (95% CI = 0–0.162).

This low EPP frequency of Nazca Boobies conforms to the expectations based on empirical data from other long-lived seabirds (Griffith et al. 2002) and theoretical considerations of the likely selection forces acting on such species (Mauck et al. 1999, Bennett and Owens 2002, Westneat and Stewart 2003). It also matches behavioral data showing that female boobies cooperate with extra-pair males in permitting extra-pair copulation; during the 8 days preceding egg-laying, however, they engage almost exclusively in within-pair copulations (DJA unpubl. data). Thus, while extra-pair copulation (EPC) is common in both the Nazca Booby (61% of females had ≥1 EPC; DJA unpubl. data) and the related Blue-footed Booby (*S. nebouxii*; Osorio-Beristain and Drummond 1998), EPP is not (see also Hunter et al. 1992, Schwartz et al. 1999). The benefits, if any, of EPC to females appear unrelated to any genetic benefits, such as fertilization insurance that could result from obtaining extra-pair sperm. This intriguing disparity between a high frequency of EPC and a low rate of EPP places the Nazca Booby in an unusual position in the spectrum of avian mating systems that merits further study.

ACKNOWLEDGMENTS

We thank the Servicio Parque Nacional Galápagos for permission to conduct this study, the Charles Darwin Research Station and TAME airline for logistical support, I. von Lippke and P. R. Sievert for field assistance, and D. F. Westneat and two anonymous reviewers for helpful comments. The University of California Agricultural Experiment Station and the Natural Science and Engineering Research Council provided financial support.

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The Wilson Journal of Ornithology 118(2):247–251, 2006

Golden-cheeked Warbler Males Participate in Nest-site Selection

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ABSTRACT.—Nest-site selection behaviors have rarely been described for songbirds. Furthermore, male involvement in nest-site selection is generally assumed to be minimal among most species, especially those predominantly exhibiting female nest building. This assumption has held true for the federally endangered Golden-cheeked Warbler (*Dendroica chrysoparia*), a breeding resident of central Texas. We observed Golden-cheeked Warbler males and females searching for nest sites together on three separate occasions, 2001–2003. Although rare, such observations add to our knowledge of the life history of songbirds. *Received 20 April 2005, accepted 11 January 2006.*

For a breeding pair of birds, the nest-site selection process can be a critical step in es-

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tablishing a pair bond; certainly, the site selected will often affect the pair's reproductive success (Martin 1998). The final choice of nest placement, whether made by the male, female, or both, will likely be influenced by several factors (e.g., local resource availability [presence of nesting materials, food], inter- and intraspecific competition, and habitat features influencing microclimate, brood parasitism or predation) that contribute to the quality and quantity of fledglings reared (Martin and Roper 1988). Recent literature on this topic has focused on gaining a better understanding of the relationship between nest placement and predation (e.g., Wilson and Cooper 1998, Siepielski et al. 2001, Boulton et al. 2003, Davis 2005)—the leading cause of reproductive failure in birds and a significant selective force on avian breeding behaviors (Ricklefs 1969, Martin 1992). Far less attention has been given to how birds actually select a site.

Information on the behavioral processes involved in nest-site selection for wood warblers, including the federally endangered Golden-cheeked Warbler (*Dendroica chrysoparia*), is generally lacking (Morse 1989, Ladd and Gass 1999). In a review of *The Birds of North America* series, we found that information on the nest-site selection process is well described for only 15 of the 51 wood warblers (families Parulidae and Peucedramidae). Furthermore, among species predominantly exhibiting female nest building, the role of the male in nest-site selection is often assumed to be minor (Kaufman 1996, Ladd and Gass 1999). With few exceptions (see Ficken 1964, Meanley 1971, Nolan 1978), males have been observed only mate-guarding and singing subdued, infrequent songs, while females actively engage in nest-site selection activities (Pulich 1976, Guzy and Lowther 1997, Wright et al. 1998).

Few data exist on the nest-site selection processes of Golden-cheeked Warblers (Ladd and Gass 1999), although aspects of their breeding biology and nesting characteristics have been described in detail (Bent 1953, Pulich 1976, Ladd and Gass 1999). The Golden-cheeked Warbler is a habitat specialist with a limited range. Its nesting habitats are closed-canopy, low-growing woodlands dominated by mature Ashe juniper (*Juniperus ashei*) and oaks (*Quercus* spp.; Ladd and Gass 1999). Such habitats are restricted to limestone slopes, canyons, and adjacent uplands in the Edwards Plateau and Llano Uplift of central Texas (Pulich 1976, Kier et al. 1977). Nests are constructed by the female with strips of mature Ashe juniper bark and are typically placed in Ashe junipers, but sometimes in oaks or other hardwoods. Nests are usually located in the upper two-thirds of a tree, averaging 5–7 m above ground (Pulich 1976).

In the only comprehensive study of Golden-cheeked Warblers, Pulich (1976) wrote that the male might accompany the female in her search for a nesting site. He described an observation made on 1 April 1961, in which a female—paying no attention to her mate—flew to the ground and picked at unidentified objects, briefly investigated an old nest in a juniper, and flew across a ravine to another tree; the male guarded his mate, actively chased an approaching satellite male, and sang infrequently. Pulich (1976) concluded that the female chooses the nest site, but he gave no description of the behavioral repertoire involved in her selection of the site. Pulich (1976:82) did acknowledge that he had likely missed some sexual displays that play a role in establishing the pair bond because "the courtship of the Golden-cheeked Warbler seems to be carried on in utmost secrecy." In another study, Golden-cheeked Warbler males were observed presenting strips of juniper bark to their mates, but courtship displays were not observed prior to nest building (Lockwood 1996).

Here, we document male and female Golden-cheeked Warblers actively searching for nest sites together on Fort Hood, an active U.S. Army installation in Bell and Coryell counties, Texas (31° 10′ N, 97° 45′ W). We recorded these events during a 3-year study involving detailed behavioral observations of color-banded Golden-cheeked Warbler males.

On 2 April 2003 at 13:15 CST, a Golden-cheeked Warbler male was heard singing the "A-song," a song-type associated with male-female interactions (Bolsinger 2000). The pair was observed displaying nest-site *trying* behaviors (Ficken 1964) in several tree forks within a cluster of shin oaks (*Q. sinuata*). *Trying* behaviors were characterized by both the male and the female squatting simultaneously or alternately in potential nearby sites while vigorously pivoting clockwise and counterclockwise. Pivots, consisting of half-rotations (180°) and up to two full rotations (720°), included outward and downward extension of wings and upward elevation of the tail. Extension of the limbs may have provided tactile information about the suitability of the site (Nolan 1978).

Interruptions to *trying* pivots included pressing the breast, belly, and sides against limbs as if "nest-shaping," attentively examining the site, or hopping to other prospective sites (all within the same shin oak cluster). At times, the female appeared to gather information from her "advertising" mate and responded to his *trying* behavior by approaching the potential nest site as soon as he left. In general, female nest-site inspection behaviors seemed to be more persistent than those of her mate, who infrequently sang a muted A-song, exhibited mate-guarding behavior, and paused more often. These activities lasted ~180 sec.

On 4 April 2003 at 11:05, we observed the same female collecting juniper strips and then flying to a nest under construction, 24 m away from the previously observed *trying* location and 4.5 m above ground in the outer branch of an Ashe juniper. The female appeared to be in her 1st day of nest construction, as a nest platform was beginning to take shape. There was no sign of her mate at that time.

Similar nest-site *trying* behaviors were recorded on two separate occasions—one in 2001 (1 April at 13:12) and one in 2002 (29 March at 10:47). In each case, we observed females in the initial phases of nest-building 3 days following our observations of *trying* behaviors. These nest-site selection activities differed somewhat from those observed in 2003 with respect to the observation duration (estimated mean for both observations = 70 sec), the degree of male participation (less in 2001; fewer pivot maneuvers in 2002, but a similar proportion of time spent hopping to prospective sites), the tree species in which nest-site *trying* took place (Ashe juniper in 2001 and 2002), and the distance between the nest-site *trying* site and the actual nest site (mean distance for both observations = 23 m).

Although detailed information on the behavioral processes of nest-site selection is rare, *trying* or *sizing* prospective nest sites—by examining the site, squatting, depressing the sternal region, nest-shaping, pivoting, elevating the tail, and extending the feet and wings—is common among several warbler species (e.g., American Redstart [*Setophaga ruticilla*; Ficken 1964], Cerulean Warbler [*Dendroica cerulea*; Oliarnyk and Robertson 1996], Prairie Warbler [*D. discolor*; Nolan 1978], and Swainson's Warbler [*Limnothlypis swainsonii*; Meanley 1971]). Reports of warbler males participating in these activities, however, are highly unusual (Morse 1989).

Our three observations of *trying* behaviors constitute the only such behaviors we witnessed during our study, and we did not observe males or females performing *trying* activities on their own. In another study, Nolan (1978) found that male Prairie Warblers behaved very much like their mates in 10% of about 300 observations. In the other 90% of Nolan's observations, the male followed and watched the female, performed display flights, and sang irregular, muted songs. Similarly, American Redstart males have been observed only occasionally *trying* sites while their mates also perform *trying* activities (Ficken 1964). Meanley (1971), Robinson (1990), and Oliarnyk and Robertson (1996) reported male Swainson's Warblers, Louisiana Waterthrushes, and Cerulean Warblers (respectively) engaged in similar nest-site *trying* behaviors with their mates, but they did not specify the frequency at which these behaviors occurred. Meanley (1971) also reported that male Swainson's Warblers might examine nest sites alone.

Interestingly, the males of species considered most closely related to Golden-cheeked Warblers (e.g., Black-throated Green Warbler [*D. virens*], Hermit Warbler [*D. occidentalis*], Townsend's Warbler [*D. townsendi*], and Black-throated Gray Warbler [*D. nigrescens*]) do not appear to participate in nest-site selection. The females either "size" or "examine" prospective sites (Black-throated Green and Townsend's warblers; Morse 1993 and Wright et. al 1998, respectively) or settle into a fork and flit around for 5–15 sec (Black-throated Gray Warbler; Guzy and Lowther 1997), while the male follows closely and infrequently utters soft songs. This apparent difference in nest-site selection strategy and display may be a function of the secretive behavior exhibited by these species during pair formation; it is certainly plausible that active male participation occurs in these species, but has simply not yet been observed. Based on well-studied warbler species, Morse (1989:169) reasoned that species' repertoires are extensive, making explicit comparisons among species difficult to derive: ". . . major differences may lie in the frequency with which a display is performed, rather than the ability to perform it." Alternatively, males of species closely related to the Golden-cheeked Warbler may not exhibit similar nest-site selection activities because visual displays in wood warblers are not necessarily correlated with phylogeny (Morse 1989). Lovette and Bermingham (1999) suggest that adaptive differences in behavioral characters exhibited by *Dendroica* species may have developed long after their explosive speciation.

Male birds may exhibit varying degrees of participation in nest-site selection by (1) selecting the site alone, (2) mate-guarding to protect their genetic investment, (3) performing displays to synchronize the pair's reproductive cycle, and/or (4) performing displays to determine an actual location that shows the most promise for successfully fledging young. Hansell (2000) suggests that increased parental care by both parents can be found among species in which both sexes build the nest together; perhaps the same holds true for species exhibiting joint male-female nest-site selection. In a review of *The Birds of North America* species accounts, we identified 96 species from 11 orders and 35 families in which both sexes actively engage in nest-site selection. Among these species, both sexes participate in feeding young in 81 (98%) of the 83 species where at least one sex feeds young. Close relatives of the Golden-cheeked Warbler, however, all exhibit biparental feeding (as is expected in nidicolous species), but do not appear to show biparental nest-site selection (Morse 1993, Guzy and Lowther 1997, Wright et al. 1998, Ladd and Gass 1999). The life-history traits (e.g., long-term pair bonds, role of sexes in parental investment) common to avian species that engage in joint male-female nest-site selection deserve additional study.

ACKNOWLEDGMENTS

We thank J. L. Sterling Graber for co-observing the 2003 nest-site selection behavior and subsequently locating the nest. We also thank numerous field technicians and volunteers, including M. Atkinson, V. Bump, B. C. Cook, K. Cutrera, J. L. Granger, K. J. Moore, H. Oswald, H. Schreiber, and R. K. Williams, who tirelessly spent hours in the field for our concurrent study dealing with the tolerance of Golden-cheeked Warblers to nonconsumptive recreation. C. M. Abbruzzesse, A. D. Anders, P. M. Cavanagh, J. D. Cornelius, D. C. Dearborn, T. J. Hayden, D. M. Herbert, S. Jester, D. L. Koehler, R. I. Leyva, B. Peak, C. E. Pekins, and M. M. Stake provided assistance with project planning, initiation, and logistical support. We thank R. T. Churchwell, S. Davis, C. G. Ladd, S. A. McClure, T. J. O'Connell, J. H. Rappole, and an anonymous reviewer for commenting on earlier versions of this manuscript. Funding for our research was provided by the Department of the Army and was administered by the U.S. Army Construction Engineering Research Laboratory and the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma State University, Oklahoma Department of Wildlife Conservation, U.S. Geological Survey, and Wildlife Management Institute cooperating). Information contained in this manuscript does not necessarily reflect the position or policy of the government, and no official endorsement should be inferred.

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The Wilson Journal of Ornithology 118(2):251–254, 2006

Provisioning of Magellanic Woodpecker (*Campephilus magellanicus*) Nestlings with Vertebrate Prey

Valeria S. Ojeda[1,2] and M. Laura Chazarreta[1]

ABSTRACT.—During the 2003–2004 and 2004–2005 nesting seasons, we studied parental behavior at seven Magellanic Woodpecker (*Campephilus magellanicus*) nests in Argentine Patagonia. Food items delivered to nestlings included wood-boring larvae (57.6%), arachnids (13.1%), and vertebrates (4.6%, including a bat, lizards, and avian eggs and nestlings). Less frequent items were adult insects, caterpillars, and pupae. Small, unidentified invertebrate prey made up 19.8% of the observations. Males delivered most of the large prey (wood-boring larvae and vertebrates; 61.7%), while females brought most of the small prey (arachnids and small, unidentified invertebrates; 79.6%), suggesting differences in foraging strategies between sexes. This is the first published account of Magellanic Woodpeckers provisioning nestlings with vertebrates. The frequency of Magellanic Woodpecker predation on vertebrates outside of the breeding seasons is unknown. *Received 26 January 2005, accepted 5 December 2005.*

Although several woodpecker species (especially melanerpine species) regularly prey on the nestlings and eggs of other birds, and a small number of species occasionally capture lizards or even mice, picids are generally not considered to be important predators of vertebrates (Short 1982, del Hoyo et al. 2002). The diet of the Magellanic Woodpecker (*Campephilus magellanicus*), the largest Neotropical picid, remains largely unstudied; the species is considered a specialist predator of large, wood-boring larvae (Short 1970, 1982). There is only one record of a Magellanic Woodpecker capturing vertebrate prey (a lizard, *Liolaemus* sp.; Ojeda 2003), and, based on what was known about the species' diet, the event was reported as opportunistic. Recent observations, however, suggest that vertebrate predation by the Magellanic Woodpecker may be more common than previously believed. Here, we present data on food

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items—including vertebrates—delivered to nestlings.

METHODS

From November to January (2003–2004 and 2004–2005 nesting seasons), we studied parental behavior of Magellanic Woodpeckers in native lenga (*Nothofagus pumilio*) forests near Bariloche (41° 08′ S, 71° 12′ W) in Nahuel Huapi National Park, Argentine Patagonia. The area is characterized by lakes, glacial valleys, and mountain slopes covered by forests dominated by southern beech (*Nothofagus* spp.). Elevations range from 400 to 3,480 m, the mean annual temperature is 8° C, and winds are predominantly westerly. Annual rainfall ranges from 500 to 2,000 mm and occurs primarily in winter (Paruelo et al. 1998).

The study was carried out at two forested sites (Challhuaco Valley and Otto Mount) located 15 km apart. Forest composition was similar between the two sites, but Otto Mount was being intensively logged at the time of our observations. Throughout the nesting season, we observed the woodpeckers' daily routine at seven nests once per week, from dawn to dusk (~06:00–21:00 UTC-3). We found one nest at the Otto Mount site and six at the Challhuaco Valley site. We made our observations from ground blinds 10–20 m from nest trees, and observed woodpeckers with 8× binoculars and a 25× spotting scope. Nests were watched for a total of 654 hr (41 days; 5–9 days/nest).

Because of marked sexual dimorphism (Short 1970) and strong territoriality (VSO pers. obs.), adults did not need to be marked. Magellanic Woodpeckers normally made one or more stops before going to the nest entrance, and once there, they perched for a few seconds before feeding nestlings. This permitted identification of the more conspicuous prey items to at least the level of class. Identification of prey to the species level was made via direct observation of predation events or during laboratory analysis of prey items found at the bottom of nest cavities (inspected every 5–10 days).

During the first 3 weeks of the nestling period, the adults normally entered the nest cavity either without prey or with items too small to be detected (Ojeda 2004). Because we saw no vertebrate prey delivered during this time, we assumed that vertebrate prey were not delivered to nestlings until they were older. Hence, the provisioning data analyzed in this paper correspond to the middle and last parts of the nestling period (nestlings 20–48 days of age, on average), when prey were large enough to be detected.

RESULTS AND DISCUSSION

We recorded 852 deliveries of conspicuous prey at seven nests. Total deliveries per nest ranged from 72 to 180. Males made 52.6% (range = 38.0–74.6%) of all prey deliveries, while females delivered 47.4% (range = 23.4–62.0%).

Most identified prey were wood-boring larvae, arachnids, and vertebrates (Table 1). Vertebrate prey was delivered to all nests, primarily by males; most "vertebrates" delivered by females were birds' eggs (n = 4). Although small sample sizes precluded statistical testing for differences in feeding behavior among pairs or sexes, large prey (wood-boring larvae and vertebrates) were mostly (61.7%) brought by males, while small prey (arachnids and unidentified small invertebrates) were mostly (79.6%) brought by females, suggesting potential differences in foraging strategies between sexes. Short (1970) proposed such differences in foraging behavior based on the species' sexual dimorphism in bill size.

Based on their slender shape and dark coloration, the lizard prey we observed were most likely *Liolaemus* sp. (N. Ibargüengoytía pers. comm.). The eggs delivered to the nests varied in coloration from white, to pink, to Niagara-green and were small- to medium-sized. Although we did not identify many of the nestling prey items (n = 14) delivered to woodpecker nestlings, at least one individual of seven species (mostly passerines) was identified: Patagonian Sierra-Finch (*Phrygilus patagonicus*), Austral Thrush (*Turdus falcklandii*), House Wren (*Troglodytes aedon*), Thorn-tailed Rayadito (*Aphrastura spinicauda*), Striped Woodpecker (*Picoides lignarius*), White-throated Treerunner (*Pygarrhichas albogularis*), and Fire-eyed Diucon (*Xolmis pyrope*). On several occasions, lizards and nestlings brought by adults were so large that they could not be swallowed by the woodpecker nestlings. In such cases, after several failed feeding attempts, the prey was left at the bot-

TABLE 1. Percentages of 852 prey items delivered by male (n = 448) and female (n = 404) Magellanic Woodpeckers (*Campephilus magellanicus*) to nestlings in seven nests in Argentine Patagonia during the 2003–2004 and 2004–2005 nesting seasons.

Prey type (n)	Both sexes	Male	Female
Invertebrates			
Wood-boring larvae (491)	57.6	65.6	48.8
Arachnids (112)	13.1	9.6	17.1
Adult insects (31)	3.6	3.3	4.0
Caterpillars (4)	0.5	0.7	0.2
Pupae (6)	0.7	1.3	0.0
Unidentified invertebrates (169)	19.8	12.0	28.5
All invertebrates (813)	95.4	92.5	98.6
Vertebrates			
Lizards (13)	1.5	2.7	0.2
Nestlings (14)	1.6	3.1	0.0
Avian eggs (8)	0.9	0.9	1.0
Bats (1)	0.1	0.2	0.0
Unidentified vertebrates (3)	0.4	0.4	0.2
All vertebrates (39)	4.6	7.4	1.5

tom of the nest cavity; on one occasion, however, an attending male flew to a nearby tree with the prey and ate it (a lizard).

The identity of avian prey or potential avian prey also was determined in several additional ways. In one case, a woodpecker provisioned its nestling with four similar, small nestlings, each brought individually. Between these deliveries, the woodpecker flew away from, and returned to, its nest from the same direction. On the last three return trips, the woodpecker was followed by a pair of Thorn-tailed Rayaditos that were vigorously harassing it, but with no effect. We interpreted this event as woodpecker predation on a brood of rayaditos. On another occasion, we witnessed a male woodpecker vigorously pecking on, and chiseling out, the bark wall that protected a House Wren nest in a natural crevice; however, the woodpecker was suddenly interrupted by his mate's arrival and he discontinued his pecking. When we examined the half-opened wren cavity, we found three small hatchlings. The adult wrens were not present during the predation attempt.

We also recorded the characteristic foraging signs of Magellanic Woodpeckers at several (n = 11) small woodpecker cavities that had been partially destroyed. Below some cavities, we observed a row of Magellanic Woodpecker feeding holes that descended from the lower lip of the cavity entrance to the floor level of the nest chamber. In other cases, it appeared that Magellanic Woodpeckers had pecked only at the level of the nest chamber's floor, where a hole about the size of the nest entrance had been drilled. Originally, these small cavities had been excavated by Striped Woodpeckers or White-throated Treerunners, and some contained the cup nests of secondary cavity nesters. Due to differences in body size and feeding habits between the Magellanic Woodpecker and these much smaller species (Short 1970, 1982), competition is not a likely explanation for the destructive behavior observed. It appears that such cavities were destroyed to reach the nest chamber at the bottom of the cavity.

This is the first published account of Magellanic Woodpeckers provisioning their nestlings with vertebrates. Though wood-boring larvae may be the primary food of this woodpecker throughout its range, there is increasing evidence that Magellanic Woodpeckers are opportunistic foragers that will take a wide variety of prey. In addition to insects, vertebrates, and eggs, they have also been recorded feeding on vegetable matter (including sap) at locations throughout much of their range (Ojeda 2003, Schlatter and Vergara 2005).

ACKNOWLEDGMENTS

We are indebted to J. M. Karlanian, M. Gelain, A. Ortíz, P. Taccari, Y. Sasal, and C. Bacchi for their indispensable assistance during the fieldwork and to N. Ibargüengoytía for her assessment concerning Patagonian reptiles. We are grateful to IDEA WILD (Fort Collins, CO, USA), Birders' Exchange (Colorado Springs, CO, USA), and J. Masello for their donations of equipment fundamental to this study. This research was supported by CANON USA through its National Parks Science Scholars Program for the Americas. We thank R. N. Conner, L. L. Short, and K. Franzreb for constructive comments that helped improve this manuscript.

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The Wilson Journal of Ornithology 118(2):254–256, 2006

Reverse Mounting and Copulation Behavior in Polyandrous Bearded Vulture (*Gypaetus barbatus*) Trios

Joan Bertran[1] and Antoni Margalida[1,2]

ABSTRACT.—We present the first report of reverse mounting in the Bearded Vulture (*Gypaetus barbatus*). The reverse mounting, which occurred in the Pyrenees of northeastern Spain, took place between the female and the alpha male in a polyandrous trio. The function of reverse mountings is discussed in relation to the previously reported high frequency of male-male mountings in this raptor species. *Received 25 April 2005, accepted 17 January 2006.*

Reverse mounting, in which the female mounts the male, has been described in a number of bird species (see James 1983, Nuechterlein and Storer 1989). This behavior has been rarely documented in raptors, however, except for a few isolated cases in species such as American Kestrel (*Falco sparverius*; Bowman and Curley 1986) and Egyptian Vulture (*Neophron percnopterus*; Donázar 1993).

We describe a case of reverse mounting in a polyandrous trio of Bearded Vultures (*Gypaetus barbatus*). Bearded Vultures are territorial and socially monogamous (Hiraldo et al. 1979); however, in the Pyrenees (in both Spain and France), where the species' largest European population occurs, polyandrous coalitions are relatively common (Heredia and Donázar 1990). The birds in this population maintained 104 breeding territories (R. Heredia and M. Razin pers. comm.), 18 of which were occupied by polyandrous trios. Before egg-laying, Bearded Vultures in the Pyrenees engage in their copulations for an average of 67 days (range = 50–90; Bertran and Margalida 1999), during which male-male mountings in trios occasionally occur (Bertran and Margalida 2003).

Between 2004 and 2005, we monitored a polyandrous trio of Bearded Vultures in the central Pre-Pyrenees mountains in Catalonia, northeastern Spain, during their courtship period (200 hr of observation). We sexed and identified the individuals by observing their

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TABLE 1. Number of male-female, male-male, and reverse mounting copulation attempts observed in monogamous pairs ($n = 8$) and polyandrous trios ($n = 5$) of Bearded Vultures in the Pyrenees, northeastern Spain, 2004–2005.

	Male-Female	Male-Male	Female-Male	Source
Pairs	189	—	0	Bertran and Margalida (1999)
Trios	356	39	1	This study

copulatory activities and specific plumage patterns. On 30 October 2004 at 12:19 UTC+1 (84 days before egg-laying), the female mounted the alpha male after she had been mounted unsuccessfully by the beta male. Following the female's mount, the alpha male drove the beta male off the perching site. The duration of the reverse mounting (8 sec) was similar to that of behaviorally successful male-female copulations recorded in other polyandrous groups (mean = 10.49 sec ± 1.30 SD, range = 8–14, $n = 37$; Bertran and Margalida 2004).

Previously, researchers have studied reverse mounting in the context of pair formation, degree of sexual motivation, or reversal of sexual dominance (Nuechterlein and Storer 1989, Bowen et al. 1991, Ortega-Ruano and Graves 1991). Due to their physical and behavioral characteristics, it has been suggested that female Bearded Vultures can dominate males (see Negro et al. 1999); in the Cattle Egret (*Bubulcus ibis*), reverse mounting has been associated with establishing dominance (Fujioka and Yamagishi 1981). However, if reverse mounting were of adaptive value (e.g., to maintain female dominance or to strengthen heterosexual couplings), it likely would be more common. On the other hand, sexual interactions outside the context of fertilization appear to be relatively common in polyandrous trios (Table 1), and reverse mounting might simply be a side effect of male-male mountings. That is, the function of reverse mounting may be to regulate socio-sexual tensions—similar to the function of male-male mountings (Bertran and Margalida 2003, see also Heg and van Treuren 1990, Cockburn 2004). Further research is needed to determine whether reverse mounting is the result of confrontational situations or helps to regulate them.

ACKNOWLEDGMENTS

We thank A. Bonada, X. Macià, P. Romero, and E. Vega for their help during fieldwork, and D. Heg and two anonymous referees for their comments. This study was supported by Departament de Medi Ambient i Habitatge de la Generalitat de Catalunya and Ministerio de Medio Ambiente.

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The Wilson Journal of Ornithology 118(2):256–259, 2006

Natural Occurrence of Crowing in a Free-living Female Galliform, the California Quail

Jennifer M. Gee[1,2]

ABSTRACT.—The vocalizations of galliform species are typically sexually dimorphic in that only the males crow. I observed crowing by a female California Quail (*Callipepla californica*), a galliform species that ranges along the Pacific coast of North America. I recorded the female crowing during a period of the breeding season when many other females were paired. The female's crow was similar in frequency to a typical male crow, though it was slightly shorter in duration. I discuss possible mechanisms and conditions that could result in female crowing. *Received 28 February 2005, accepted 21 December 2005.*

California Quail (*Callipepla californica*) show pronounced sexual dimorphism in calling behavior: males crow, whereas females do not. The California Quail's crow is commonly called the Male Advertisement or *cow* call (Sumner 1935, Williams 1969). Males usually crow early in the breeding season (Williams 1969), or when their mates are incubating or die (JMG pers. obs.). Crowing males often perch in conspicuous locations and countercall to each other. To my knowledge, there have been no previous reports of female California Quail crowing under natural conditions, although Genelly (1955) observed an instance of crowing in female California Quail that were held under captive conditions.

I observed a female California Quail crowing in the foothills of the Santa Rosa Mountains, California (33° 22′ N, 116° 15′ W), during the breeding season when many males were crowing (March 2000). In that region, the ranges of California and Gambel's (*C. gambelii*) quail overlap and hybrids or backcrosses compose approximately 60% of the population (Gee 2003). From 14 to 16 March, while conducting daily observations (>7 hr/day) at this site with a spotting scope, I observed a female California Quail crowing for 1- to 2-hr periods. This female approached to approximately 5 m in response to calls that I made with a quail call, and she continued crowing from that distance for more than 10 min. Both California and Gambel's quail are sexually dimorphic; thus, I used field markings to identify the sex and species of the crowing bird. I identified the individual as female by her lack of secondary sex traits (e.g., brown cap, black face with white margin), and as a California Quail by the presence of scaled breast feathers, forward-pointing crest, and overall blue-gray body plumage (not buff). However, backcrosses may look very similar to pure parental types (Gee 2003). I was unable to trap the bird, so I could use neither genotyping to confirm the sex or species designation nor laparotomy to examine the internal anatomical sex. Despite plumage traits, there is potentially some ambiguity as to the "true" sex and species of this individual.

I used Canary 1.2.4 (www.birds.cornell.edu/brp/SoundSoftware.html) and Syrinx (Burt 2005) sound analysis programs to digitize recordings and prepare spectrograms from which frequency and sound duration were

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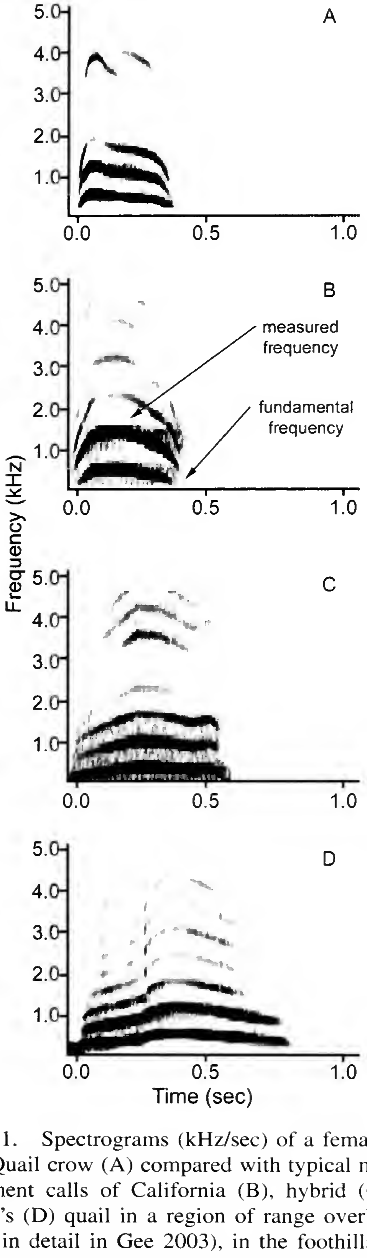

FIG. 1. Spectrograms (kHz/sec) of a female California Quail crow (A) compared with typical male advertisement calls of California (B), hybrid (C), and Gambel's (D) quail in a region of range overlap (described in detail in Gee 2003), in the foothills of the Santa Rosa Mountains, California. Recordings were made between 1998 and 2001.

measured. Many low-frequency noises obscured the first harmonic (fundamental frequency) of the call; therefore, I measured the peak frequency of the harmonic nearest the fundamental frequency because it was clearly visible in all spectrograms (Fig. 1). The female's crow was approximately the same frequency as, but slightly shorter in duration than, that of an average male California Quail (Table 1). The female exhibited male-typical crowing posture and behavior, calling from a conspicuous rock outcrop to males that were crowing in the distance. Though it was a year of moderate reproductive success, the female did not appear to have a mate, nor was she a local resident based on detailed observations of color-banded individuals at this location (for methods see Gee 2003).

Conditions and mechanisms that could have caused this female's unusual behavior include (1) elevated testosterone due to increased female competition, or (2) elevated testosterone coupled with age-dependent decrease in ovarian function and estrogen production. Note that in both cases, I suggest a role for testosterone, but without examination of the gonad, there is no way to verify the anatomical and physiological sex of the crowing, apparently female individual. Thus, a reproductive, possibly endocrine, pathology may have contributed to this behavior.

Intense competition may affect testosterone levels and crowing behavior. In males, increased testosterone occurs when males are competing for mates, and it is a normal consequence of reaching breeding condition. Similarly in females, intense competition for scarce resources, such as food or mates, could elevate testosterone levels or its rate of conversion to other steroids. When California Quail were kept in female-biased pens, females became more aggressive and began crowing, possibly due to intense competition (reported in Calkins et al. 1999). Although the sex ratio from January to June at my study site was not significantly skewed (52:48, $n = 130$), local movements could have created periods of unusually intense female competition. The crowing female was unpaired and part of a wave of transient residents, many of which appeared to be in small groups of 4–6 individuals.

Testosterone has been shown to play a role in the crowing behavior of male Gambel's Quail and female Japanese Quail (*Coturnix japonica*). In Gambel's Quail, testosterone injections administered during July (late breeding season) caused normal adult males, but not females, to call more frequently and behave more aggressively (Williams 1969). However, when female Japanese Quail were both ovariecto-

TABLE 1. Call duration and peak frequency (mean ± SD) of California, Gambel's, and hybrid quail in a region of range overlap (described in detail in Gee 2003), in the foothills of the Santa Rosa Mountains, California. Recordings were made between 1998 and 2001. Sample sizes for call duration and frequency of different males are as follows: *Callipepla californica* (8, 8), hybrid (16, 8), *C. gambelii* (11, 8). Multiple recordings were made of the calling female. Only the clearest recording was measured, although her crows appeared very similar to one another.

	Female	Male		
	C. californica	*C. californica*	Hybrid	*C. gambelii*
Duration (sec)	0.36	0.38 (0.03)	0.45 (0.02)	0.53 (0.03)
Frequency (kHz)	1.98	2.03 (0.16)	1.85 (0.17)	1.86 (0.90)

mized and treated with testosterone, they crowed and strutted similar to males (Adkins and Adler 1972; Adkins 1975; Balthazart et al. 1983, 1996). Thus, two factors may cause female crowing: increased levels of testosterone and decreased ovarian function. Ovarian function appears to diminish with age in Gambel's and California quail, as evidenced by the acquisition of partial male plumage among some older females (Hagelin and Kimball 1997) and the finding that sexually dimorphic plumage is estrogen-dependent in many galliforms (Domm 1939, Owens and Short 1995). In the case reported here, the age of the crowing female was unknown, and she showed no evidence of partial male plumage. Although both vocalizations and plumage could be affected by ovarian function, female crowing and partial male plumage are not coupled and are likely regulated by different mechanisms. Vocalizations appear to be governed, in part, by increased numbers of androgen receptors in the vocal control regions or by steroid-converting enzymes. For example, administering the aromatase inhibitor, fadrazole, results in crowing by female Japanese Quail (Marx et al. 2004). Similarly, the crowing and strutting of male Japanese Quail largely depend on the conversion of testosterone to dihydrotestosterone and on androgen receptors (Adkins-Regan 2005).

In the sympatric population I studied, male-typical plumage is infrequent (but consistently present) in female California, Gambel's, and hybrid quail, while male-typical vocalizations are not. Approximately 1% of the banded female California, Gambel's, and hybrid quail have partial male plumage, and they may pair and breed normally (JMG pers. obs.). In contrast, I observed only one female with male-typical calling patterns. This difference suggests that separate mechanisms govern sexually dimorphic plumage compared to sexually dimorphic vocalizations, but it also suggests that different selective pressures may act on plumage and crowing. The consequences of female crowing may be severe, particularly if crowing is associated with other aggressive and territorial behaviors, as it is in both New World quail (Johnsgard 1988) and Japanese Quail (Balaban 1997). Thus, female crowing may occur only under the rare circumstances when it and other aggressive behaviors—which are typical among reproductive males—do not decrease the reproductive fitness of female quail.

ACKNOWLEDGMENTS

Financial support was provided by a National Science Foundation Predoctoral Fellowship; a National Science Foundation Doctoral Dissertation Improvement Grant DEB-0073271; an Environmental Protection Agency Science-to-Achieve-Results Graduate Fellowship U-91572901-0; Sigma Xi Grants-in-Aid of Research; the American Ornithologists' Union Betty Carnes Memorial Award; and The Reserve Community Association of The Reserve, Palm Desert, California. Carolyn Stillwell helped to draw figures. For comments, I thank S. M. Correa, M. L. Tomaszycki, J. C. Hagelin, and three anonymous referees.

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The Wilson Journal of Ornithology 118(2):259–261, 2006

Poult Adoption and Nest Abandonment by a Female Rio Grande Wild Turkey in Texas

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ABSTRACT.—While evaluating reproductive parameters in Rio Grande Wild Turkeys (*Meleagris gallopavo intermedia*) in the Edwards Plateau region of Texas, we observed a case of poult adoption and abandonment of an active nest. In wild turkeys, adoption of poults has been described previously, but during our observation the hen also abandoned her nest at a late stage of incubation. Most research discussing adoption in gallinaceous birds has focused on brood abandonment after hatch. Although poult adoption in conjunction with nest abandonment is probably rare, our observations indicate that it can occur, at least in Rio Grande Wild Turkeys. *Received 7 June 2005, accepted 16 February 2006.*

Species such as gulls (*Larus* spp.), terns (*Sterna* spp.), and geese (*Branta* spp.) readily adopt offspring (Pierottie and Murphy 1987, Saino et al. 1994, Larsson et al. 1995). Northern Bobwhites (*Colinus virginianus*) utilize brood abandonment and adoption as a strategy for increasing nesting opportunities (Burger et al. 1995, DeMaso et al. 1997), but documented cases of gallinaceous birds adopting offspring are rare (Martin 1989, Mills and Rumble 1991). Adoption of poults by Merriam's Wild Turkeys (*Meleagris gallopavo merriami*) has been described (Mills and Rumble 1991), and Healy (1992) reported nest abandonment

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by a captive hen that was attracted to the calls of another brood. In May 2005, we observed a Rio Grande Wild Turkey (*M. g. intermedia*) hen adopt a poult and then abandon her own nest in Kerr County, Texas. To our knowledge, adoption in conjunction with nest abandonment has not been documented before in the wild.

As part of a study to evaluate the reproductive ecology of Rio Grande Wild Turkeys in Texas, we tracked a radio-tagged juvenile hen through two nesting attempts on the Kerr Wildlife Management Area in Kerr County (30° 04′ N, 99° 20′ W), Texas. On 11 April 2005, we found her first nest, which contained 13 eggs, and we estimated nest age at 3 days. On 15 April, the nest was depredated, and the hen subsequently renested on 28 April. After 28 April, we checked the hen's nesting status ≥5 times per week. On 7 May, the second nest contained 12 eggs and nearby we set up an infrared trail camera (Moultrie Game Spy™) to monitor the nest. From 8 to 21 May, we never observed the hen off the nest, and, based on our intensive tracking of the hen, there was no possibility that she hatched this poult several days early.

At 16:00 CST on 21 May, we found the hen incubating her second nest. On the following day at 11:00, we located the hen about 600 m from the nest. We approached to ~15 m of the hen and observed her bedded down in a grassy area dominated by little bluestem (*Schizachyrium scoparium*). Upon further approach, she flushed. Within about 1 min, a poult, estimated to be 4 days old, ran from the grassy area where the hen had been bedded. We then examined the hen's nest and found all 12 eggs present and intact. We also floated the eggs and estimated that they were at day 23 of incubation (Healy 1992).

On 23 May, we relocated the radio-tagged hen in an effort to catch and radio-tag the poult; however, the hen was moving and we were unable to locate the poult. On the following day, the hen was relocated again, this time with the poult. On 26 May, we captured the poult, estimated its age as 9 days, radio-tagged it with a 1.2-g poult transmitter (Bowman et al. 2002; Advanced Telemetry Systems, Isanti, Minnesota), and released it.

Other than anecdotal evidence and the article by Mills and Rumble (1991), there is little available information on the frequency of adoption in wild turkeys. Whereas Mills and Rumble (1991) reported poult adoption by turkey hens both with and without existing broods, the hen we observed had abandoned her clutch of 12 eggs after considerable investment (≥20 days of incubation) to care for a single poult. While such cases of abandonment and adoption are probably rare, our observations indicate that it can occur in Rio Grande Wild Turkeys. Possible causes might include hen physiological condition or changes in photoperiod (Scanes et al. 1979, Youngren et al. 1993, Bedecarrats et al. 1997, Sharp et al. 1998). The hen that we observed was in the latter stages of incubation on a second nest when the adoption event occurred; thus, her levels of luteinizing hormone and prolactin may have changed sufficiently to promote behavioral changes (i.e., poult-rearing behavior in preference to continued incubation). Additional research is needed to clarify what might trigger simultaneous poult adoption and nest abandonment in turkeys.

ACKNOWLEDGMENTS

Funding for this project was provided by the Texas Turkey Stamp Fund through the Texas Parks and Wildlife Department, the National Wild Turkey Federation, and the Department of Wildlife and Fisheries Sciences, Texas A&M University. This research was conducted under Texas A&M University Animal Use Permit No. 2005-005. We appreciate the comments from three anonymous reviewers that improved this manuscript.

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The Wilson Journal of Ornithology 118(2):261–263, 2006

Predation by a Blue-crowned Motmot (*Momotus momota*) on a Hummingbird

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ABSTRACT.—We describe predation of a Green-crowned Brilliant (*Heliodoxa jacula*) by a Blue-crowned Motmot (*Momotus momota*) in southern Costa Rica. We did not witness the capture of the hummingbird, but did observe the motmot swallow the prey whole. Although the diet of the Blue-crowned Motmot is highly variable and can include birds, this is the first report of predation on an adult hummingbird. *Received 27 January 2005, accepted 4 December 2005.*

Members of the family Momotidae have been observed eating a wide range of fruits, arthropods, and small vertebrates (Meyer de Schauensee 1964, Ridgely and Gwynne 1989, Stiles and Skutch 1989, Karr et al. 1990, Remsen et al. 1993). Although Remsen et al. (1993) indicate that arthropods, supplemented by fruits, are the more important component of motmot diets, vertebrates have also been found in the stomachs of some Momotidae species (Wetmore 1968, Stiles and Skutch 1989). Specifically, motmots have been observed eating poison dart frogs (Master 1999), snakes (Stiles and Skutch 1989), mice (Delgado-V. and Brooks 2003), and bats (Chacón-Madrigal and Barrantes 2004).

The Blue-crowned Motmot (*Momotus momota*), found throughout the lowlands and middle elevations (to ~1,500 m) of Costa Rica (Stiles and Skutch 1989), forages on large spiders, earthworms, insects, nestling birds, and small snakes and lizards (Stiles and Skutch 1989, Henderson 2002). There are, however, no known accounts of motmots eating adult birds. Here, we describe predation on an adult hummingbird by a Blue-crowned Motmot.

The incident occurred on the morning of 27 February 2004 at the Las Cruces Biological Field Station (8° 47′ N, 82° 57′ W) of the Organization for Tropical Studies in San Vito, Coto Brus, Puntarenas, Costa Rica (elevation

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= 1,100 m, annual rainfall = 3,988 mm). (For a full description of the site, see Mintken and Gunther 1991 and Spencer 1991). At 07:30 CST, we observed a motmot—perched on the cement stairs in front of a station building—with a Green-crowned Brilliant (*Heliodoxa jacula*) in its bill. The motmot held the hummingbird by its body and repeatedly beat it against the cement. The hummingbird appeared freshly dead and was easily identifiable. As we did not witness the capture, the hummingbird may have been dead or injured prior to capture, although there are no accounts of motmots eating prey they did not kill.

At 07:35, the motmot flew to the ground ~7 m away and continued to beat the hummingbird against the ground. At 07:40, it moved under a building and beat the hummingbird against a rock for almost 1 min. As a result, most of the hummingbird's feathers were lost and its bill was broken. At 07:43, the motmot moved out from under the building to a grassy area with some tree cover and continued to beat the hummingbird against the ground. At this point, the motmot was 7 m from its mate, which was perched on a tree branch 2 m high and present for the entire period; it did not make any attempt to move closer to the motmot with the hummingbird. The motmot never used its feet to manipulate or hold the prey; the entire time it held, turned, and manipulated the hummingbird only with its bill.

At 07:54, the motmot attempted, but failed, to swallow the hummingbird whole. The motmot threw the hummingbird on the ground, picked it up again with its bill, and continued to beat it against the ground. At 07:56, the motmot again tried to swallow the hummingbird and was successful. It held the hummingbird by the back and swallowed it back end first. The motmot then flew to a tree branch and perched near its mate.

Reported sources of adult hummingbird mortality include arthropods (e.g., Butler 1949, Hildebrand 1949, Carignan 1988, Graham 1997), frogs (Monroe 1957), and several avian taxa: small raptors (e.g., Lowery 1938, Mayr 1966, Stiles 1978), Great Shrike Tyrants (*Agriornis livida*; Martinez del Rio 1992), Baltimore Orioles (*Icterus galbula*; Wright 1962), and Dusky-green Oropendolas (*Psarocolius atrouirens*; Graves 1978). Ours is the first report of a Blue-crowned Motmot eating an adult bird of any kind. Our observation is best explained as an opportunistic event and broadens the range of predators that kill and eat hummingbirds.

ACKNOWLEDGMENTS

We would like to thank K. G. Murray for helpful comments on earlier drafts of the manuscript. T. L. Master, J. V. Remsen, and an anonymous reviewer made invaluable comments. The Organization for Tropical Studies provided logistical support at Las Cruces Biological Station.

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The Wilson Journal of Ornithology 118(2):264–266, 2006

Once Upon a Time in American Ornithology

Alexander Wilson, namesake of *The Wilson Journal of Ornithology,* was born on 6 July 1766 in Scotland. There, he trained and worked as a weaver (and a poet). In 1794, he emigrated to the U.S., and for 9 years he worked as a teacher. His own education had been sketchy, however, and he had to study to teach. Eventually, North America's birds and wilderness held him—there were more birds and species than in his native Scotland. Eager to begin a life work, Wilson set out on 1 June 1803 to draw "all the finest birds of America." For the next 10 years, he wrote and illustrated his seminal work, *American Ornithology,* the first scientific treatment of American birds and the first to stress natural history and field biology. He had an untaught skill in painting, but William Bartram, America's foremost naturalist and a neighbor in his hometown of Philadelphia, taught him how to draw. Bartram also answered Wilson's natural history queries, and inspired and instructed him in ornithology, botany, and bird illustration.

Wilson was still teaching in 1805, but art and science dominated his thoughts as his drawing improved. He took a job as an assistant editor with a publishing house in 1806 and ultimately convinced the publisher to support his developing work, but only if Wilson could get commitments from 250 subscribers at $120 each. On 7 April 1807, a brochure for *American Ornithology* was sent to 2,500 of the most eminent people in the U.S.

As time allowed, Wilson traveled extensively, widening his knowledge of birdlife and gathering information on the distribution, nesting habits, and movements of North American birds. He often traveled on foot or by horseback, and while accumulating bird lore, always equipped himself with a shotgun, paint, paper, sketching materials, and a notebook. Wilson made four great adventures—through dense forests and swamps, across Indian territory, and in all seasons—traversing every state in the Union, often alone, in search of birds and subscribers. On his first trip, October to December 1804, he traveled 1,300 miles from Philadelphia to Niagara Falls and back, mostly on foot, but also by stagecoach, skiff, and sloop. Then, in September 1808, he was off to New England in search of birds and subscribers willing to commit $120 for his *American Ornithology.* During the winter of 1808–1809, he continued his fieldwork and search for subscribers, traveling south by horseback to Maryland, New Jersey, Virginia, North and South Carolina, and Georgia. Wilson's longest expedition began in January of 1810, when he went from Philadelphia to Pittsburgh, then south on the Ohio River to Louisville in a skiff (that Wilson christened "Ornithologist"), then overland to Natchez, through hostile Chickasaw Indian territory, and finally on to New Orleans.

The list of subscribers to Wilson's *American Ornithology* included some of the greatest personalities of his time: President Thomas Jefferson, Robert Fulton (inventor of the first commercial steamship), and Thomas Paine. Wilson also enlisted the assistance of Meriwether Lewis, who provided bird specimens—collected during his remarkable 1804–1806 expedition with William Clark—from which Wilson could draw birds of western origin.

Wilson died of dysentery at the age of 47 in 1813, just before publication of the 8th volume of *American Ornithology.* The 9th and last volume was compiled by George Ord from Wilson's notes and drawings.

It was on a trip through the southern coastal states that Wilson recorded the following ornithological observation. On 2 February 1809, 12 miles outside Wilmington, North Carolina, he collected two Ivory-billed Woodpeckers (*Campephilus principalis*), and slightly wounded a third (a male). Wilson's illustrations of the Ivory-billed Woodpecker (Fig. 1) in his *American Ornithology* came from drawings he made of the injured bird while in his Wilmington hotel room. The original reference is: Brewer, T. M. 1840. Wilson's American Ornithology, with notes by Jardine. Otis, Broaders, and Co., Boston, Massachusetts.—JAMES A. SEDGWICK; e-mail: jim_sedgwick@usgs.gov

FIG. 1. Wilson's Ivory-billed Woodpecker (top right, bottom center), Pileated Woodpecker (top and bottom left), and Red-headed Woodpecker (bottom right). Illustrations of the Ivory-billed Woodpecker were drawn from a live bird that Wilson took to his hotel room in Wilmington, North Carolina, in 1809. Color plate from: Wilson, A. 1829. American ornithology; or, The natural history of the birds of the United States. Collins & Co., New York. Image courtesy of the Josselyn Van Tyne Memorial Library, University of Michigan, Ann Arbor.

The first place I observed this bird at, when on my way to the south, was about twelve miles north of Wilmington in North Carolina. There I found the bird from which the drawing of Fig. 131 was taken. This bird was only wounded slightly in the wing, and, on being caught, uttered a loudly reiterated and most piteous note, exactly resembling the violent crying of a young child; which terrified my horse so, as nearly to have cost me my life. It was distressing to hear it. I carried it with me in the chair, under cover, to Wilmington. In passing through the streets, its affecting cries surprised every one within hearing, particularly the females, who hurried to the doors and windows with looks of alarm and anxiety. I drove on, and, on arriving at the piazza of the hotel, where I intended to put up, the landlord came forward, and a number of other persons who happened to be there, all equally alarmed at what they heard; this was greatly increased by my asking, whether he could furnish me with accommodations for myself and my baby. The man looked blank and foolish, while the others stared with still greater astonishment. After diverting myself for a minute or two at their expense, I drew my Woodpecker from under the cover, and a general laugh took place. I took him up stairs, and locked him up in my room, while I went to see my horse taken care of. In less than an hour, I returned, and, on opening the door, he set up the same distressing shout, which now appeared to proceed from grief that he had been discovered in his attempts at escape. He had mounted along the side of the window, nearly as high as the ceiling, a little below which he had begun to break through. The bed was covered with large pieces of plaster; the lath was exposed for at least fifteen inches square, and a hole, large enough to admit the fist, opened to the weather-boards; so that, in less than another hour, he would certainly have succeeded in making his way through. I now tied a string round his leg, and, fastening it to the table, again left him. I wished to preserve his life, and had gone off in search of suitable food for him. As I reascended the stairs, I heard him again hard at work, and on entering had the mortification to perceive that he had almost entirely ruined the mahogany table to which he was fastened, and on which he had wreaked his whole vengeance. While engaged in taking the drawing, he cut me severely in several places, and, on the whole, displayed such a noble and unconquerable spirit, that I was frequently tempted to restore him to his native woods. He lived with me nearly three days, but refused all sustenance, and I witnessed his death with regret.

The Wilson Journal of Ornithology 118(2):267–276, 2006

Ornithological Literature

Compiled by Mary Gustafson

BIRDS OF BELIZE. By H. Lee Jones, illustrated by Dana Gardner. University of Texas Press, Austin. 2003: 317 pp., 56 color plates with facing-page figure captions, 234 range maps, 28 numbered figures. ISBN: 0292740662, $60.00 (cloth). ISBN: 0292701640, $34.95 (paper).—Being a country where English is spoken, and which still retains 70% of its native habitat, it is no surprise that Belize is an increasingly popular destination for ornithologists and birders alike. In fact, hundreds of birders visit this tiny country annually to enjoy its rich avifauna, natural beauty, and amazingly friendly residents. For the past decade, ornithologists and birders visiting Belize were served quite well by Howell and Webb's *A Guide to the Birds of Mexico and Northern Central America* (Oxford University Press, 1995). As masterful as that work is, however, the 851-page tome weighs in at a hefty 3.4 lbs., a bit much to carry in the field. A much more portable, but clearly outdated, option is Peterson and Chalif's *A Field Guide to Mexican Birds* (Houghton Mifflin, 1973). Now there is a third option: *Birds of Belize* is the first guide to comprehensively cover all 574 species known to occur in this birder-friendly country. All regularly occurring species are illustrated, including North American migrants that spend only part of the year in Belize. Neither Peterson and Chalif nor Howell and Webb illustrate North American migrants, and both guides include many Mexican species that do not occur in Belize. For anyone who is not thoroughly familiar with bird distribution in Central America, the convenience of having only Belizean birds in one volume is difficult to overstate. *Birds of Belize* is also two-thirds the weight of Howell and Webb, though still a bit large to easily tote in the field. The guide's format is traditional and easy to use, with plates and brief, facing-page text in the front; more-comprehensive text and detailed maps are in the back. The facing-page text covers not only identification notes, but also the species' status, distribution, and habitat—incredibly useful information found in few other guides. Probably the greatest strength of this guide is its superb, authoritative text. Lee Jones's knowledge about the birds of Belize is unsurpassed. He gives excellent descriptions of status, distribution, and general identification features for each species. His notes on habitat are particularly helpful for anyone seeking a particular species, and his descriptions of vocalizations are unusually complete, accurate, and helpful. For those seeking more in-depth information on a particular subject, a comprehensive bibliography is available.

For better or worse, the quality of a field guide depends, to a large degree, on the quality of its illustrations. The illustrations in this guide are attractive and, in most cases, more than adequate to convey the important identifying characters. In general, Neotropical resident species are better illustrated than North American migrants; plates of antbirds, wrens, becards, and tanagers are particularly lovely and accurate. For some of the more difficult ID questions, however, the illustrations fall short and other sources may need to be consulted. For example, all the raptors in flight are misshapen and the plumage markings of many are incorrect. Those in Howell and Webb are far superior. Likewise, the *Leptotila* doves, which are best identified by general color pattern, look too similar: Gray-fronted Dove (*L. rufaxilla*) should be more rufous-brown above with contrasting gray nape and head; White-tipped Dove (*L. verreauxi*) should be more gray-brown; and Gray-chested Dove (*L. cassini*) should have a more contrasting gray breast. Again, those in Howell and Webb are much better.

For many of the North American migrants, such as shorebirds, gulls, and terns, one would be much better served by consulting some of the better North American references such as *The Sibley Guide* (Alfred A. Knopf, 2000). Indeed, the juvenile Red-footed Booby (*Sula sula*), the small *Calidris* sandpipers, the Common (*Sterna hirundo*) and Roseate (*S. dougallii*) terns, the *Empidonax* flycatchers, the immature Cape May Warbler (*Dendroica tigri-*

na), and the basic-plumaged Palm Warbler (*D. palmarum*) are probably not identifiable from their illustrations in *Birds of Belize*; the juvenile Yellow-crowned Night-Heron (*Nyctanassa violacea*) should show pale-edged wing coverts and a black bill; the juvenile Black-crowned Night-Heron (*Nycticorax nycticorax*) has shorter legs than those portrayed; the *Myiarchus* flycatchers are too dark and small-headed with incorrect wing patterns (see Sibley or Howell and Webb for better illustrations). The shapes are a bit off on many species: note especially that the Clay-colored (*Spizella pallida*), Chipping (*S. passerina*), Lincoln's (*Melospiza lincolnii*), and Savannah (*Passerculus sandwichensis*) sparrows are all shown with similar proportions, including identical tail lengths. In life, these species differ markedly in proportions (see Sibley). Countless other small mistakes make some of the illustrations less useful than they could be.

The text has a few minor shortcomings. Whereas habitats are nicely described, there is little or nothing about habits of birds: how they move, how they feed, what they eat, whether they are easy or hard to see, how they nest. Although such information may be somewhat limited for many Neotropical species, what is known for any one species could have been included in a few short lines without making the book much larger—particularly since the line spacing was larger than it needed to be. It is also unfortunate that the text was printed on heavy, glossy paper, which added unnecessary weight and thickness to the book.

Several aspects of the guide's layout could have been improved. Most notably, bird sizes should have been indicated on the plates. Size, after all, is a critical starting point in the identification process. Also, it is impossible to go quickly from the plates to the maps. One must go from the plates to the text to find out what page the map is on. The maps themselves are a bit confusing. Supposedly, range maps for species that occur throughout Belize are not included, which undoubtedly saves space but may be confusing for someone not familiar with the birds of the region. Plus, some maps for colonial waterbirds are misleading. For example, the Great Egret (*Ardea alba*) map is illustrated with four dots indicating the locations of breeding colonies, yet there is no indication of where foraging birds occur outside (or during, for that matter) the breeding season. Other species, such as Red-footed Booby, which clearly has a more limited nonbreeding distribution than Great Egret, are mapped in a similar way. Rarities for which there are few records are not mapped, which is also understandable; however, a number of species that occur regularly in parts of Belize, such as Black-crested Coquette (*Lophornis helenae*), are not mapped. The migration distribution is not mapped for any species, though it certainly would have been helpful.

Although less than perfect, *Birds of Belize* is still an attractive, authoritative, and very useful guide. Its positive attributes far outweigh its shortcomings. It serves as a handy reference for Belizean birds and is recommended as the guide of choice to most birders visiting this splendid country.—MICHAEL O'BRIEN, WINGS, Inc., West Cape May, New Jersey; e-mail: tsweet@comcast.net

ARIZONA BREEDING BIRD ATLAS. Edited by Troy E. Corman and Cathryn Wise-Gervais. University of New Mexico Press, Albuquerque. 2005: 646 pp., 5 figures, 12 tables, 336 photographs (53 habitat photos, 281 bird photos), 281 maps, 270 habitat charts, 194 phenology graphs. ISBN: 0826333796. $45.00 (cloth).—State breeding bird atlases get better and better. Arizona's raises the standard once again. Authoritative species accounts, illustrated with generous use of color, make presentation of data thorough, clear, and vivid. Atlas workers (atlasers) recorded 283 breeding species, plus 19 potential breeders. The 270 main species accounts brim with atlas-derived information, more than many state atlases provide.

Each 2-page account features the usual state map, with easy-to-discern color-coding to depict the three confidence levels portraying the likelihood of breeding within a given atlas block. The block statistics summarize the number of priority blocks and topographic quads (1:74,000-scale maps) in which field workers recorded the species. Color photographs supply the obligatory depiction of birds in the species accounts. Each account also includes two informative charts: a breeding phenology chart (for species with adequate data) and a graph depicting habitat use.

Arizona's atlas project specified 40 habitat types within seven habitat landscapes (tundra, forests and woodlands, scrublands, grasslands, desert lands, wetlands, and urban/agricultural). Illustrated with color photographs, a preliminary chapter on habitat describes each of the 40 habitats and reports on status and distribution. Many habitats, especially those in desert systems, suffer declines attributable to human activities and exacerbated by Arizona's burgeoning population.

Unlike some other atlases in which phenology charts report the range of dates in which atlasers recorded each stage of breeding (i.e., atlas breeding phenology codes), phenology charts in the Arizona Atlas simply report overall breeding activity. The atlas also highlights an interesting facet of Arizona bird life—the summer "monsoon" season in July and August. Monsoons stimulate second nestings by such species as Canyon Towhee (*Pipilo fuscus*), Rufous-crowned Sparrow (*Aimophila ruficeps*), Eastern Meadowlark (*Sturnella magna*), and maybe Common Yellowthroat (*Geothlypis trichas*), as well as the first and only nestings by Cassin's (*Aimophila cassinii*), Botteri's (*Aimophila botterii*) and Grasshopper (*Ammodramus savannarum*) sparrows, Varied Bunting (*Passerina versicolor*), and possibly Lazuli Bunting (*Passerina amoena*).

Three topics organize the species accounts: Habitat, Breeding, and Distribution and Status. Under Habitat, authors, referring briefly to habitat preferences reported by previous authors, analyze the principal habitats in which atlasers found the species. The Breeding section leads with short expositions about breeding biology, often derived from the *Birds of North America* series, and compares these precepts with atlas observations.

The Distribution and Status section reports on the species' seasonal status, and then compares atlas findings with previous works on Arizona, particularly the seminal work by Allan Phillips, Joe Marshall, and Gale Monson, *The Birds of Arizona* (University of Arizona Press, 1964) and—for species occurring primarily in Mexico—*The Birds of Sonora* by Steve Russell and Gale Monson (University of Arizona Press, 1990). The discussion details where and with what frequency field workers detected the species, provides comments on its detectability, and concludes with an analysis of the species status and conservation standing.

One slightly distracting theme in many species accounts involves a small section of Arizona where the Apache Nation refused atlasers access to tribal lands. Their section of the White Mountains (east-central Arizona) contains one of Arizona's few areas of high-elevation habitat. Authors of species accounts frequently lament the lack of coverage in the missing priority blocks (30 out of 1,834) and often project species' likely ranges in the missing blocks.

Some species accounts contain a unique feature: measurements of nest-site characteristics. Field workers measured or described characteristics of 3,507 nests of 184 species, including nest height and nest tree. For example, atlasers found 121 Phainopepla (*Phainopepla nitrens*) nests in 17 tree species (almost half in palo verde, *Parkinsonia* sp.) at a median height of 2.4 m (range = 1–10 m).

Nineteen authors contributed species accounts, although the editors wrote most of them. They follow an admirably consistent style with comparable contents, although an editor's eye might pick out a few grammatical goofs (e.g., hanging participial phrases that most readers will not notice) and a few typos.

The first part of the book discusses the details of atlas organization, methods, limitations and biases, and summarizes the results. One chapter covers geography, climate, and habitats, and another offers a brief history of Arizona ornithologists. (The first recorded bird observations came from Coronado's expedition in 1540–1542, although we do not learn what he claimed to see.) It concludes by quoting Elliot Coues' sharing "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."

The summary of results appropriately starts by recognizing the 710 field workers (those who surveyed one or more atlas blocks) and 422 block helpers, who put in 51,737 hr of field work (plus 18,119 hr of travel time). Blocks with the most species are distributed along a northwesterly line from the southeastern corner of Arizona to the center of the state, from the Chiricahua and Huachuca mountains north to the White Mountains, and west along the Mogollon Rim as far as Prescott. Mourning Dove (*Zenaida macroura*) heads the list of species reported in the most blocks, followed by Ash-throated Flycatcher (*Myiarchus cinerascens*), House Finch (*Carpodacus mexicanus*), Common Raven (*Corvus corax*), Red-tailed Hawk (*Buteo jamaicensis*), Northern Mockingbird (*Mimus polyglottos*), Black-throated Sparrow (*Amphispiza bilineata*), and Brown-headed Cowbird (*Molothrus ater*). Arizona specialties in the top 21 include Cactus Wren (*Campylorhynchus brunneicapillus*), Phainopepla, and Verdin (*Auriparus flaviceps*).

In many states, atlas field workers have succeeded in surveying remote and rugged regions that avian researchers ordinarily do not study. In Arizona, their efforts have expanded, or filled in, the known ranges of many species. In contrast, they have also identified several declining species, including Buff-breasted Flycatcher (*Empidonax fulvifrons*), American Dipper (*Cinclus mexicanus*), and Evening Grosbeak (*Coccothraustes vespertinus*). Many species accounts detail declines due to habitat destruction—especially the loss of saguaros (*Carnegiea gigantea*) felled by wildfires and urbanization. Atlas results show that a surprising number of species have a limited range in Arizona—aside from the Mexican species that occasionally wander northward into the southeastern mountains. Overall, this atlas provides fascinating, thorough, accessible information about Arizona's unique breeding avifauna—HUGH E. KINGERY, Franktown, Colorado; e-mail: ouzels@juno.com

NESTING BIRDS OF A TROPICAL FRONTIER: THE LOWER RIO GRANDE VALLEY OF TEXAS. By Timothy Brush. Texas A&M University Press, College Station. 2005: 245 + xiv pp., 31 color photographs, 11 color illustrations, 2 tables, 5 maps. ISBN: 1585444367, $50.00 (cloth). ISBN: 1585444901, $24.95 (paper).—The Lower Rio Grande Valley of Texas is well known to ornithologists and birders alike who have an interest in the avifauna of the United States. Many species of birds with a more tropical distribution reach the northern portion of their range in southern Texas, and the Valley, as it is often referred to, offers easy accessibility to the habitats that these birds occupy. The geographic area covered includes the four southern-most counties in Texas: Cameron, Hidalgo, Starr, and Willacy. The two eastern counties—Cameron and Willacy—and southern Hidalgo County are part of the recently formed delta of the Rio Grande; thus, the land use is largely devoted to row-crops. For a variety of reasons, the remainder of the Valley is less conducive to agriculture and, historically, ranching has been the primary industry. During the past 2 decades, the human population in these four counties has steadily increased and subsequent urbanization is readily apparent. Conservation agencies, both public and private, have made great efforts to protect remaining patches of native vegetation, particularly in the eastern half of the Valley. These four counties cover approximately 1.2 million ha and can boast an avifauna of just over 500 documented species.

As the title states, this book focuses on the breeding avifauna of the Lower Rio Grande Valley of Texas. The majority of the book takes a narrative format that is easy to read and discusses all species that either breed regularly or occasionally within the area. At the beginning of the book, there is a short section that includes color photos of selected species as well as several habitat shots. Compelling among these are aerial photos of Santa Ana National Wildlife Refuge taken prior to the construction of Falcon Dam (in 1953) and in 1981 to compare changes in the condition of the Rio Grande and surrounding land use. The remainder of the color section includes several paintings by Gerald Sneed depicting various nesting birds of the Valley. These paintings provide something that photos can't convey, the feeling of being in the Valley's natural habitats.

The introductory chapters provide a baseline understanding of the Lower Rio Grande Valley. There are overviews of topography and climate, as well as an interesting historical perspective of land use and its effect on ecological diversity. Two of the remaining chapters in the introductory section include a brief discussion of the basic habitats found in the study area and seasonal changes in the avifauna. A highlight of the book is the extensive

References section, which will be a great help to anyone working on the avifauna of South Texas. The bulk of the book is composed of species accounts.

The accounts include all species (171) for which there is at least one acceptable breeding record. At the time of writing, Eurasian Collared-Doves (*Streptopelia decaocto*) were just beginning to arrive in the Valley, but have now taken hold and can be added to that list. As might be expected, the lengths of species accounts vary greatly. Brush gives extended coverage to species that are South Texas specialties and other species that may be of particular interest due to their behavior, ecology, or changes in relative abundance. The longer species accounts form the heart of the book and contain fairly detailed information about the natural history of those species in the Valley. Accounts of the remaining species vary in length, with most including mention of the habitats used by the specific species. Brush specifically mentions that the style of the species accounts is a hybrid between standard regional works and other natural history writing that relies heavily on personal experiences and field notes. In many ways, this adds interesting aspects to the species accounts in which Brush has particular interest, such as Green Parakeet (*Aratinga holochlora*), Northern Beardless-Tyrannulet (*Camptostoma imberbe*), Tropical Parula (*Parula pitiayumi*), and Altamira Oriole (*Icterus gularis*).

My main quibble with the book is that some species that are irregular breeders in the Valley are covered very briefly, sometimes with only a couple of lines. I would have liked to see more detailed information on these occurrences. I also question the inclusion of Yellow-faced Grassquit (*Tiaris olivaceus*) as having a breeding record in Texas. In my mind, a single male building a "nest" does not qualify as a nesting attempt, but this is a minor point. In the introductory section of the book, Brush does point out that there are five subspecies endemic, or nearly endemic, to the Tamaulipan Biotic Province; in the species accounts, however, more detailed information is not included for all these taxa. He does discuss the "Brownsville" Common Yellowthroat (*Geothlypis trichas insperata*) and other subspecies that occur in the Valley, although I would have liked a more in-depth treatment of these taxa, such as that given to the Valley specialties. If more research is needed on these taxa, this would have been a good opportunity to point out major gaps in the current knowledge. As mentioned previously, Brush relies heavily on his own field experience in the Valley, thereby adding a nice dimension to the book for those taxa with which he has personal experience. For other species, however, his brief notes don't always add to the account. Overall, I found the book to be very informative and would recommend it to ornithologists and birders alike who are interested in the avifauna of Texas.—MARK W. LOCKWOOD, Texas Parks and Wildlife Department, Fort Davis, Texas; e-mail: mark.lockwood@tpwd.state.tx.us

BIRDS OF WASHINGTON: STATUS AND DISTRIBUTION. Edited by Terence R. Wahl, Bill Tweit, and Steven G. Mlodinow. Oregon State University Press, Corvallis. 2005: x + 436 pp., 285 maps. ISBN: 0870720494. $65.00 (cloth).—State avifaunal works used to be the province of professional ornithologists working for the U.S. Biological Survey, other government agencies, or universities. In recent years, as ornithological research has moved into physiological, molecular, and evolutionary hypothesis testing, faunal investigation and summarization increasingly have been delegated to dedicated and talented nonprofessionals. This volume was developed by a team of 46 authors, including the 3 editors. Many have biological training and employment, but I doubt that working on this book fit into any of their job descriptions.

Birds of Washington includes a short introductory section, followed by species accounts for about 482 accepted species. The wrap-up includes a brief discussion of non-established introduced species, including accounts for Mute Swan (*Cygnus olor*), Mandarin Duck (*Aix galericulata*), American Black Duck (*Anas rubripes*), Monk Parakeet (*Myiopsitta monachus*), and eight species of hypothetical occurrence. Appendices include a table of occurrences by habitat and brief biographies of the 46 authors.

This book serves an important function as an up-to-date status check on bird occurrence, distribution, abundance, and changes therein. The included material appears reliable and authoritative, but I am frustrated by what is not included. This is a bare-bones treatment with minimal analysis presented. The introductory material includes an explanation of the species account format, a full page of abbreviations used, a chapter by Christopher Chappell on *Bird Habitats of Washington*, one on *Avian Conservation* by Joseph Buchanan, a brief discussion of the history of field ornithology in Washington, a description of the recent information sources used, and slightly more than a page on changes in status and distribution over the past half-century. The habitat chapter provides a listing and descriptions of 30 habitats and a lucid explanation of the basis for their delimitation. All of the other sections left me wishing for more detail. The history chapter essentially begins with Jewett et al.'s *Birds of Washington State* (University of Washington Press, Seattle, 1953) and does not even mention W. L. Dawson, who wrote the monumental first state bird books for Washington and California. The *Changes in Status and Distribution* section lacks a discussion of the number of species occurring in Washington, or the rate of addition of new species. The treatment of increases and decreases in range and abundance describes general classes of causes and gives examples, but without enough detail to really give a reader much sense of the magnitude or prevalence of these changes.

The species accounts for regularly occurring species begin with a brief statement of status in Washington. Abundance categories are based on likelihood of encounter rather than estimates of actual numbers present. A graphic illustrating seasonal occurrence and relative abundance follows, then a listing of subspecies in Washington, if more than one, and a listing of the habitats used. A section titled *Occurrence* provides detail on distribution, abundance, and changes thereof. An optional *Remarks* section is followed by *Noteworthy Records*, which includes high counts and unusual dates. Authorship is acknowledged for the accounts of accepted species but not for those of introduced and hypothetical species. Very detailed distribution maps—based mainly on the distribution of suitable habitat—accompany 283 of the accounts. Seasonal changes in distribution are indicated with different shades of gray.

Vagrants receive much shorter accounts, which list their occurrences in Washington and sometimes a little information on the species' normal distribution and abundance. The term "casual vagrant" is used in place of the traditional "accidental" for the species with the fewest records. Inclusion as an accepted species is based on acceptance by the Washington Bird Records Committee. Corroborating evidence is usually mentioned, but up to 30 species appear to be accepted based only on observer descriptions (the text is not always clear on this). I imagine that most of these records were accurate, but several (e.g., Little Curlew, *Numenius minutus*; Ruby-throated Hummingbird, *Archilochus colubris*; Mourning Warbler, *Oporornis philadelphia*; Nelson's Sharp-tailed Sparrow, *Ammodramus nelsoni*) present non-trivial identification issues. Citations for many of the records of rarities refer to the Records Committee reports rather than the original sources. The locality information for Washington records often lacks county or other regional reference, so someone not familiar with Washington geography will need a good gazetteer to locate Asotin, Crockett L., Stanwood, Twisp, Wallula, and so on.

This book will be useful to Washington birders interested in the status of the birds they see. It will also be of interest to scholars interested in dynamics of biogeography, range expansion, range contraction, and vagrancy. Unfortunately, the editors apparently did not recognize this latter audience, and have not made the information of interest to scholars as accessible as they could have.—WAYNE HOFFMAN, Newport, Oregon; e-mail: whoffman@peak.org

PEREGRINE FALCON: STORIES OF THE BLUE MEANIE. By James Enderson, original art by Robert Katona. University of Texas Press, Austin. 2005: 266 pp., 18 photographs, 23 line drawings. ISBN: 0292705905, $65.00 (cloth). ISBN: 0292706243, $22.95 (paper).—Professor Emeritus James Enderson of Colorado College has written an engaging and very readable memoir that centers on the decline and recovery of the Peregrine Falcon (*Falco peregrinus*), a now-revered raptor that suffered near extinction in much of its range beginning in the mid-20th century. The dramatic and remarkable recovery of this species in North America, following the banning of DDT, is certainly one of the most significant conservation victories of the last century, and Jim Enderson was a major player on a team that won the game. The book's illustrations include well-chosen black and white photographs, as well as many original drawings by artist Robert Katona, whose contributions add significantly to the book's success.

Enderson's account might well be required reading for young ornithology students; certainly, it must be that for graduate students and established professionals. Enderson tells his story well, and much of the ground he covers in this book is now covered with actual or allegorical asphalt, no longer accessible to students currently embarking on careers. The stars that crossed for Enderson were falconry and science. He clearly has a passion for both, and he was able to weave threads from each to build a career full of adventure, scientific puzzle-solving, and a cast of characters that might have come from a novel.

The introductory chapter is a splendid description of the Peregrine Falcon, certainly "one of the best-studied wild animals on the planet." (*The Birds of North America* species account lists over 300 references.) Enderson provides us with an excellent summary of this remarkable species' speed, biology, sexual dimorphism, coloration, distribution, hunting techniques, and other critical life-history components. The nickname "Blue Meanie"—used throughout the book—is credited to Enderson's fellow peregrine researcher and good friend, W. Grainger Hunt.

Enderson's story begins in the early 1960s with his searches for falcons. He focused at first on Prairie Falcons (*Falco mexicanus*), then (like all falconers of that era) dreamed of peregrines. His chance to engage with peregrines was finally realized when two falconers invited him to visit the Queen Charlotte Islands off the British Columbia coast, which at the time was the site of the densest population of nesting peregrines anywhere in their cosmopolitan range. One suspects that Enderson's rappelling skills might have had something to do with the invitation, but the story of the expedition is wonderful autobiography and adventure. Even in his quest for falconry birds, Enderson's scientific orientation shines through. For example, the expedition guide shot a harbor seal (*Phoca vitulina*) to feed nestling peregrines recently taken from the wild and, in describing the butchering, Enderson cannot resist the temptation (or obligation) to tell us why the seal's flesh was so dark (it relates to storing high levels of oxygen when diving). He went home with his first peregrine—the most highly valued species in the world of American falconry.

By that time, Enderson was a graduate student, and soon thereafter landed a job at Colorado College, in part because of his connection with Robert Stabler, a professor at the college and a famous pioneer falconer. Peregrines had been declining for a decade, but the picture was blurred in part by the secrecy that surrounded nest sites—those who knew the bird were not eager to tell their stories, and most attributed local declines to egg collectors or falconers. (In California, a few of us who watched nesting peregrines knew that eggs had been laid, but when we later returned to cliffs, the adults defended weakly or not at all, and the nest ledges were empty. At one site where a friend had lavished a landowner with canned hams and whiskey in an attempt to exclude the reviled "eggers," we concluded that the egg-collectors had come in from the sea!) Surveys were then initiated (which turned out to be post-decline surveys), and Enderson was one of the first surveyors. He checked some 50 historical nesting sites, largely in the intercontinental West, and found only 13 pairs. The picture would worsen before it was over.

The watershed event was the Peregrine Conference of 1965, where peregrine scientists and falconers assembled in Madison, Wisconsin, to assess the extent of the decline and speculate on the reasons for it. Enderson was there and he was much impressed by what he saw. Hypotheses explored as possible causes of decline included: the peregrine is a "wilderness species," egg collecting, falconers, drought, and pesticides. Enderson omits mention of Rachel Carson (*Silent Spring* was published in 1962), and fails to point out that there was significant resistance to even discussing pesticides at the conference. Roger Tory Peterson was sitting not far from me, and at one frustrating moment when the inevitable discussion about pesticides was sidestepped by a U.S. Fish and Wildlife Service representative, a frustrated and angry Peterson stabbed the table with his wooden pencil!

But Enderson tells the DDE story well. It was indeed like a mystery novel, with the primary culprit being DDE, not DDT, or dieldrin, or any other of the array of biocides that Carson had described in *Silent Spring*. As Enderson describes it, there were many dead-end roads traveled, in part because DDE was not toxic to insects; therefore it had been little investigated. It turned out to be the primary culprit that caused eggshell thinning and was responsible for most of the population decline. The proof would not emerge until the parent compound DDT was banned, but along the way, experimental science provided strong evidence. Enderson rightly credits David Peakall with discovering DDE in peregrine eggshells that were collected in 1948, only a couple of years after the "wonder insecticide" had been introduced into general agricultural use.

Some of the best parts of Enderson's book are his stories of peregrine surveys in North America, and eventually in other parts of the world. Enderson participated in many, if not most, of these surveys, and his tales of canoeing Arctic rivers, dangling from ropes on 500-foot cliffs, and interacting with sundry bureaucrats make good reading. He tells wonderful tales of remarkable characters, often with a little spice and always with excellent descriptions of character. For example, put in the care of a "surly sergeant" on a Texas beach when he is trapping migrating peregrines, Enderson wins the day by trapping, banding, and releasing four birds. The surly sergeant had been assigned to drive Enderson (and Clayton White, another giant in the peregrine story) as punishment, but ended up an enthusiastic trapper. There are tales of many others.

Enderson was also part of the group that managed, at long last, to breed falcons in captivity. In a chapter titled *Timely Invention of Peregrine Husbandry*, Enderson describes this technology in detail (I could have done without the illustrated description of collecting peregrine semen in the seam of a rubber gasket placed on the head of the collector!). Then (remarkably), he describes his theft of nestling peregrines from some of the last productive eyries in the United States and Canada. It was a matter of the means justifying the ends, one supposes, but it may raise some eyebrows.

Enderson—such an intimate part of the captive breeding and release program that is widely credited with "saving the peregrine"—points out that what really saved the species was the (then) controversial decision in 1972 by William Ruckelshaus, head of the new Environmental Protection Agency, to ban most uses of DDT. He also asserts that the Peregrine Falcon would have recovered on its own from the small reservoir of functional breeding pairs left here and there, but it would have taken much longer, especially in those areas from which it had disappeared entirely. The release program was very popular, and resulted in the elevation of the peregrine to the status of absolute charisma. It had gone from the reviled, often shot "Duck Hawk" of the mid-20th century to one of the best-loved, wild vertebrates in the world.

Falconry is a major topic in this book, and Enderson does it justice. He describes the sport's early days in North America, the colorful cast of characters, and the discovery of the Arctic Peregrine's Atlantic and Gulf of Mexico coastal migration paths. He even includes a primer on falconry, which gives the reader a sense of what that passion is all about. I was especially pleased to see that Enderson favors the correct pronunciation of falcon: these birds are not "*phal*-cons," but "the historically correct '*fall*-cons,' as in the word *falling*." A "*phal*-con" is a car or a football team; a "*fall*-con" is a bird.

In the latter passages, Enderson brings falconry up to date and describes—with appropriate bitterness—"Operation Falcon," a federal sting operation that, between 1981 and 1984, entrapped some 52 falconers and confiscated 106 raptors. It was an unfortunate chapter in the peregrine story.

One serious omission hangs over Enderson's book—a fuller coverage of those who sought to obfuscate the developing truth about DDE, including pesticide company employees. Mention, perhaps, should also have been made of the false claims that the peregrine's decline was faked by scientists who stood to benefit (in terms of professional fame and research money) by reporting the precipitous decline in numbers of peregrines.

This excellent book ends with a nicely written memory of peregrines having returned to two historical nesting sites from which they had been missing for decades. The writing here is a splendid description of emotional encounters with nature. The reader is put at the spot and in the experience, and when blue meanies appear after seemingly fruitless searches, one shares in the relief and exultation. In an era when radiotelemetry has partially replaced old-fashioned fieldwork and modeling is thought to be a substitute for much of what has occupied biologists for ages, Enderson's book reminds us of why most of us enter wildlife-related work in the first place. In most cases, we love the wild things we study, we admire their beauty, and we do all we can to guarantee that succeeding generations will be able to do the same.—STEVEN G. HERMAN, The Evergreen State College, Olympia, Washington; e-mail: hermans@evergreen.edu

HAWKS FROM EVERY ANGLE. By Jerry Liguori. Princeton University Press, Princeton, New Jersey. 2005: 133 pp., 68 plates, 371 photos, 2 maps. ISBN: 0691118248, $55.00 (cloth). ISBN: 0691118256, $19.95 (paper).—In his new book, *Hawks from Every Angle,* Jerry Liguori uses a new and different approach to identify 19 migratory hawk species in flight. In the introduction, Jerry writes, "This is primarily a visual guide; the photos and captions are the crux of the book and are meant to stand on their own." Unlike previous photo guides that offer images showing every field mark in perfect lighting at point-blank range, Jerry has selected high-quality images that more accurately reflect true conditions of field observation. He used his extensive experience studying hawks throughout North America to select images that reflect realistic flight profiles and structures for each species. Through these images, Jerry represents the full range of varying postures the birds can show in flight when viewed from differing angles and under varying environmental conditions.

Multiple images are often stitched together and presented side by side, with as many as six images per page representing a single "plate." These stitched images typically show comparative views of similar species at the same angle, differing plumages (age, sex, morph, race) of a given species, or different flight profiles that illustrate the range of variation for a given species under varying conditions. The accompanying captions smartly describe these comparative differences. The author uses a holistic approach to identification similar to that seen in *Hawks in Flight* by Pete Dunne, David Sibley, and Clay Sutton (Houghton Mifflin, 1988), except Jerry opts for images over written descriptions as the primary focus of the guide. As such, this guide is more useful in the field than its predecessor, which was meant to be read at home.

The book is clearly designed for use by hawkwatching enthusiasts at hawkwatching sites. In the introduction, Jerry summarizes a number of sites across North America, graphs peak migration times by species, and adds tables that summarize high counts, by species. The images generally cover the entire range of expected "looks" each species may offer as it flies by any hawkwatch site. However, when pictures alone won't suffice, Jerry uses intuitive descriptions of behaviors, such as comparative differences in wing flapping and flight characteristics. For example, "Sharp-shinned Hawks beat their wings in a shallow, snappy, powerless manner, similar to a Robin. . . . Cooper's Hawks almost always soar with a slight dihedral. . . . In moderate to high winds, Sharp-shinned Hawks appear hyperactive, unstable, and hesitant, making constant wing adjustments." These subjective differences are used by seasoned hawkwatchers on a daily basis to identify distant raptors, but they are gleaned from thousands of hours of experience and are not included in typical guides. The author generally excludes fine details not easily seen in the field such as eye color, and descriptions of individual feathers that are notable only at very close range.

The text is organized by species and presented in a consistent format (the three accipiter species: *A. striatus*, *A. cooperii*, and *A. gentilis* are treated as one group with comparative differences highlighted throughout). Each species account begins with a general overview of the species (or species group), followed by sections on migration and plumage, respectively. The remainder (and bulk) of the account is dedicated to Flight Style with subsections including wing beat, soaring, head-on, gliding overhead, and wing-on/going away. Portions of these accounts can be difficult to follow at times, particularly in the accipiter section, which continually bounces between the three species; however, the author addresses this, to a degree, by using bold print to accentuate key points and distinctive characteristics found throughout.

As anyone familiar with raptors might expect, maximum coverage was given to the highly variable Red-tailed Hawk (*Buteo jamaicensis*). Jerry uses a full 14 pages of text and images to thoroughly cover a wide range of recognized subspecies, races, forms, and color morphs in each age class. Jerry also covers the varying age classes of Bald Eagle (*Haliaeetus leucocephalus*) and Golden Eagle (*Aquila chrysaetos*) with detailed descriptions of molt sequences and other plumage characteristics.

This guide offers as much insightful commentary on flight characteristics of raptors as any guide ever has. It also offers a greater range of differing perspectives and flight profiles than any previous guide. Unfortunately, despite the all-encompassing title, there are some "angles" not covered. For example, there is no mention or images of perched birds, and there is no coverage of general natural history other than that pertaining to migration. The exclusion of some field marks definitely limits the scope and usefulness of this book as well.

Whereas this book is clearly an indispensable resource for anyone interested in hawkwatching, away from the hawkwatch site it offers little assistance for the observer wanting to identify the hawk perched in their backyard. It also offers little for those curious about nesting habits or breeding range of a given species. For answers to these questions, readers will have to turn to another guide. However, if the backyard hawk flies from the tree and you are able to observe it as it flaps straight away, then *Hawks from Every Angle* is likely just the ticket. Given the reasonable price, slim profile, and the wealth of personal wisdom packed into the pages of this book, it deserves a spot on every birder's bookshelf. There is no one who can't learn something from this work!—JEFFREY BOUTON, Leica Sport Optics, Port Charlotte, Florida; e-mail: jbouton2@earthlink.net

THE WILSON JOURNAL OF ORNITHOLOGY

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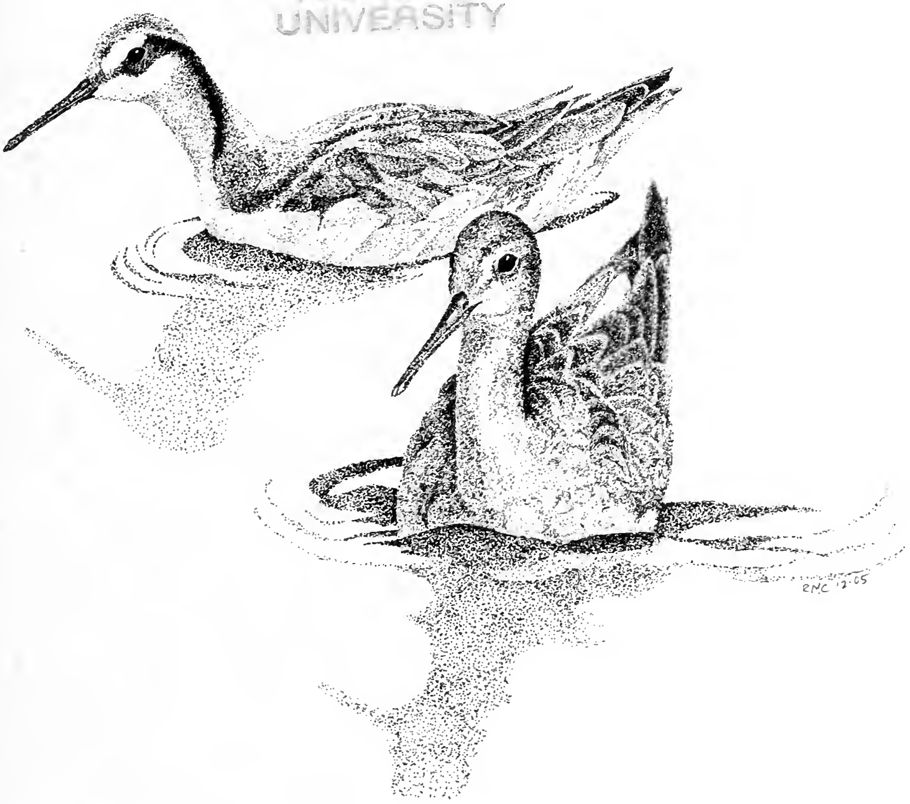

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Wilson Ornithological Society

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THE WILSON JOURNAL OF ORNITHOLOGY
(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th St., Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Blvd., Ste. 680, Waco, TX 76710.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

COVER: Wilson's Phalaropes (*Phalaropus tricolor*). Illustration by Robin Corcoran.

FRONTISPIECE. American Dippers (*Cinclus mexicanus*) nesting in the Oregon Coast Range exhibit flexibility with respect to selecting nest sites. By constructing nesting substrates (nest boxes, ledges on cliffs) to augment the availability of natural sites, Loegering and Anthony (p. 281) increased the number of actively used nesting sites from three to eight along a 10-km reach of stream. Original painting (mixed media: gouache water color and acrylic) by Barry Kent MacKay.

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 118, NO. 3 September 2006 PAGES 281–438

The Wilson Journal of Ornithology 118(3):281–294, 2006

NEST-SITE SELECTION AND PRODUCTIVITY OF AMERICAN DIPPERS IN THE OREGON COAST RANGE

JOHN P. LOEGERING[1,2,3] AND ROBERT G. ANTHONY[1]

ABSTRACT.—Availability of high-quality nest sites is thought to limit breeding populations of American Dippers (*Cinclus mexicanus*). To examine this hypothesis, we characterized dipper nest sites, nest-site habitat, and productivity in the central Oregon Coast Range. We also made additional nest sites ("created" nest sites = nest boxes, cliff ledges, hollowed logs that we constructed or created) along one of two creeks. Suitable nest sites (1) provided a physical space to place the nest, (2) were above the upper reach of flooding and inaccessible to ground predators, and (3) were very near to, or extended over, the stream's edge. Given these requirements, and within the context of swift, unpolluted mountain streams, dippers exhibited flexibility in their nest-site selection patterns and used a variety of nesting substrates. Streamside features associated with dipper nest sites included geomorphically constrained valleys (i.e., narrow valley floors), the presence of trees in the riparian zone (not tested statistically, but nearly universal to all nest sites), stream shading from overhead vegetation, and locations that were farther from areas frequented by humans (e.g., roads). Dippers readily used nesting substrates that we created, more than doubling the breeding population on a 10-km reach of stream (8 versus 3 nests/10-km reach). Reproductive success was high and not associated with any habitat feature we measured. The factors influencing recruitment in the Oregon Coast Range remain unknown. *Received 6 October 2004, accepted 5 May 2006.*

Habitat associations of many terrestrial species associated with streams in the Pacific Northwest are lacking (Anthony et al. 1987; McGarigal and McComb unpubl. data), but are essential for ecologically sound management. The American Dipper (*Cinclus mexicanus*) is the most abundant resident, riparian-obligate bird species in managed forests of the central Oregon Coast Range (Loegering and Anthony 1999). From Alaska to Panama, dippers are widely distributed in mountainous regions of western North America and Central America (Bent 1948, Kingery 1996). Generally, nest sites are located over, or near the edges of, streams, where they are inaccessible to predators and often sheltered from the weather (Hann 1950, Price and Bock 1983, Kingery 1996). More specifically, the nests—constructed with moss and enclosed with a domed roof (15–25 cm in diameter)—typically are placed on cliff ledges; on ledges of mid-stream boulders; in crevices be-

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tween boulders; in cavities of horizontal, hollow logs extending over streams; under or within the support structure of bridges (Kingery 1996, Osborn 1999, Morrissey 2004); or in nest boxes (Hawthorne 1979).

Price and Bock (1983) suggested that dipper reproductive success may vary with nest-site quality, but this possibility remained untested. We characterized and evaluated dipper nest-site selection in the central Oregon Coast Range at three spatial scales (Johnson 1980): (1) microhabitat (approximately 0.25–1.0 m^2 around the nest), (2) macrohabitat (approximately 1–10 m^2 around the nest), and (3) streamside habitat (>100 m^2 around the nest). Specifically, we characterized dipper microhabitat and macrohabitat and tested the null hypotheses that (1) streamside habitat at dipper nests was not different from that of randomly selected locations; (2) reproductive success was not correlated with any features of nest-site habitat at the microhabitat, macrohabitat, or streamside scales; and (3) increased availability of nest sites would not affect the number of breeding pairs. Because nest-site availability has been suggested as a factor limiting dipper populations (Price and Bock 1983, Kingery 1996), we also experimentally increased the number of available nest sites along one stream and monitored nest densities there and along an unaltered stream for 5 years.

METHODS

Study area.—During the 1993–1998 breeding seasons, we studied dippers along Drift (44° 25′ N, 123° 50′ W) and Lobster (44° 15′ N, 123° 40′ W) creeks in the central Oregon Coast Range, Oregon, and, in 1994, along 23 additional streams in 6 basins within a 10-km radius of Drift and Lobster creeks. During 1994 we searched 181 km of streams to locate nest sites and collect microhabitat, macrohabitat, and streamside habitat data. During 1993–1995, we studied reproductive success only on Drift and Lobster creeks. During 1993–1998, we censused the abundance of nests, and we studied occupancy of natural nest sites and those that we made only on Drift and Lobster creeks. These basins were located in Benton, Lane, and Lincoln counties and drained into the Alsea and Siuslaw rivers 6 to 23 km east of the Pacific Ocean. Streambed elevations ranged from 3 to 365 m, and the topography was characterized by steep terrain interspersed with moderately flat valleys. Stream gradient averaged $<4\%$, (range $= 0.5–11\%$), generally increasing in the smaller, fourth-order streams (“stream order” is a stream classification system: first-order streams are small, unbranched tributaries; two first-order streams join to make a second-order stream, and so on; Strahler 1957, Everest et al. 1985:201). We surveyed 91.4 km of fourth-order, 50.6 km of fifth-order, and 39.0 km of sixth-order streams, the mean widths of which were 4.2 m (range = 1–30 m, $n = 203$ randomly selected points along Drift and Lobster creeks), 10.1 m (range = 2–25 m, $n = 203$), and 16.2 m (range = 3–38 m, $n = 100$), respectively. The maritime climate was characterized by mild, wet winters and cool, dry summers. Annual precipitation was 180–300 cm, 75–85% of which fell during October–March. Mean temperature seldom fell below 0° C in the winter, and summer temperatures rarely exceeded 27° C (Franklin and Dyrness 1973).

Vegetation upslope of riparian areas in the Coast Range was characteristic of the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973) and was dominated by subclimax Douglas-fir (*Pseudotsuga menziesii*), western hemlock, western red cedar (*Thuja plicata*), and red alder (*Alnus rubra*). Upslope seral stages ranged from recently harvested to mature forests (trees >200 years old). Riparian areas were typically forested by red alder, Douglas-fir, bigleaf maple (*Acer macrophyllum*), and western red cedar.

Microhabitat and macrohabitat.—We searched for active and old dipper nests in 1994 ($n = 51$) along Drift and Lobster creeks and along the 23 additional streams to characterize microhabitat, macrohabitat, and streamside habitat characteristics. We surveyed all streams on foot and searched within 5 m of the water's edge for all sites capable of supporting a nest (hereafter, nest site), including mid-stream boulders, debris jams, rootwads, logs >30 cm in diameter, bridges, cliffs, and steep banks. We collected microhabitat, macrohabitat, and streamside habitat data at every site. Microhabitat variables measured at nest sites on cliffs included height, width, and depth of the supporting ledge; the average thickness of moss on the ledge or cliff; indicators of shelter from the weather (typically overhanging vegetation or a rock overhang), terrestrial predator access, and whether the site had a near-horizontal ledge or platform $>10 \times 10$

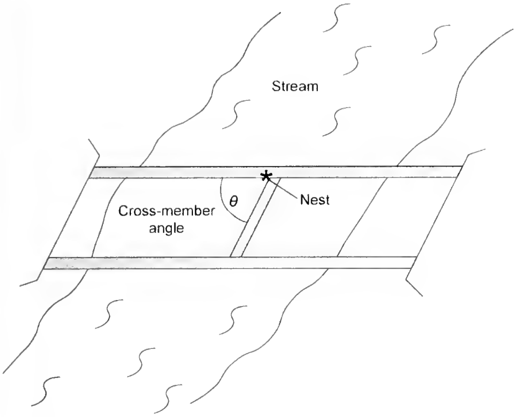

FIG. 1. Illustration of a typical mountain stream bridge in the Oregon Coast Range, showing the support beams and cross member. Typical American Dipper nest location (*) and cross-member angle (θ, ≤90°) also are shown.

cm. We considered a nest inaccessible to terrestrial predators if the nest ledge did not extend horizontally to the surrounding upslope, was >1 m high or perched out over the stream, and the cliff was smooth enough to thwart climbing predators, such as American mink (*Mustela vison*). We defined macrohabitat variables as cliff height and length, cliff slope or verticality (90° was exactly vertical, cliffs <90° sloped away from the stream, and cliffs >90° sloped out over the stream's edge), and cliff vertical area (area of cliff face that was ≥90°). We also recorded height of the ledge or nest above the ground or streambed, the height from nest to an overhang above (if present), and the horizontal distance from the nest to stream edge at base winter flow (hereafter, setback distance). Setback distance was zero for nests placed directly above the edge of the stream, positive for nests placed over dry land, and negative for nests positioned over the stream. We used winter base flow because dippers selected breeding sites in February and March (JPL pers. obs.) when streams were at this level. For nests in logs or log cavities, macrohabitat variables also included the diameter of the log and whether or not the log was coniferous. For nests at bridges (n = 11 with nests, n = 11 without), we also recorded the cross-member angle, which was the acute angle (i.e., ≤90° in a horizontal plane) formed by the cross member and one of the load-bearing beams (θ in Fig. 1). In our study, dipper nests on bridges typically were placed in this acute angle formed by the load-bearing support beam and the cross member.

To assess the availability of nest sites that were suitable but not used by dippers, we identified every site in our study basins that appeared suitable—based on sites described in the literature (Price and Bock 1983, Kingery 1996) and from our own experience—but did not currently hold a nest (n = 42). We erred on the side of possibly including unsuitable sites rather than conservatively excluding sites that might have served as nest sites. We characterized the microhabitat and macrohabitat at these sites, but did not compare them statistically to known nest sites.

Streamside habitat.—In 1994, we measured seven variables (stream shading, distance to human activity, valley form, adjacent land use, canopy cover, stream bank vegetation, and riparian zone vegetation) to characterize and compare streamside and riparian zone habitat at all active and old nests (n = 22) and at 506 randomly selected locations along Drift and Lobster creeks. Streamside habitat was not assessed at nests in other basins. None of the randomly selected locations had a dipper nest present or the microhabitat and macrohabitat suitable for a dipper nest. We visually estimated stream shading as the percentage of a transect across the stream that was shaded from directly overhead. Distance to human activity was estimated as the straight-line distance (m) to areas frequented by humans (e.g., roads, dwellings, etc.). We defined valley form as either constrained (valley floor <2 × the width of the active channel) or unconstrained (valley floor >2 × the width of the active channel). Adjacent land use was classified as either managed forest or other (e.g., residential, agriculture, pasture, wilderness area, or campground). We visually estimated canopy cover (nearest percent) in a 5-m-diameter plot 25 m from the stream. We characterized streambank (immediately adjacent to the stream) and riparian zone (25 m from the stream) vegetation according to the dominant overstory species, whether the dominant vegetation was composed of mature trees (woody vegetation >5 m tall versus structurally simpler, non-tree vegetation), and whether the vegetation was coniferous. Thus, there were four categories of dominant vegetation: conifer trees (e.g., Douglas-fir, all size classes >5 m tall), non-conifer trees (e.g., red alder), non-tree conifers (e.g., Douglas-fir, 0–15 years, <5 m tall), and non-tree, non-conifers (e.g., shrubs, grasses, and forbs). For the analyses, we used two binary variables (tree versus non-tree; conifer versus non-conifer) to simplify this vegetation assessment. We referred to Hitchcock and Cronquist (1973) to identify vegetation.

Productivity.—During 1993–1995, we searched for and monitored active dipper nests along Drift and Lobster creeks to assess reproductive success (n = 16 nest sites and 48 nesting attempts over the 3 years). We examined all nests of both first and second broods at least weekly, noting the number of eggs, chicks, or fledged young, and often checked nests more frequently near the estimated fledging date, as recommended by Stanley (2004). Chicks were uniquely color banded at 10–14 days of age, and hatching dates were based on nest-initiation dates and growth characteristics indicative of chick age (Sullivan 1973). We considered a nest or brood successful if at least one egg hatched or at least one chick fledged, respectively. The number of eggs hatched was determined during the first visit to the nest following hatching, and we estimated the number of chicks fledged by counting the number of recently fledged young near the nest during or after fledging. If no fledged young were observed, we assumed number fledged to be equal to the number of young present at the previous nest check as long as the previous nest check was ≥20 days after hatching, and there were no signs of nest disturbance. We also identified sources of nest failure whenever possible.

Created nest sites.—In August 1993 and 1994, we constructed nine nest structures (five nest boxes, two log cavities, and two cliff ledges; hereafter referred to as "created" nest sites) along a segment of Drift Creek (9,480 m long) and compared dipper nest abundance to that along a comparable portion of Lobster Creek (7,800 m long)—an unaltered control—to assess nest site availability and saturation. Both reaches were similar in size, gradient, geomorphology, and adjacent land use. We constructed nest boxes (Loegering 1997) similar to those used by Hawthorne (1979) in California and Jost (1970) in Europe. The open cavities were made by using a brace and bit in the ends of two, nearly horizontal logs extending over the stream (minimum dimensions were 15 × 19 × 15 cm). We used a hammer and chisel to construct two ledges on sandstone cliffs lacking a mossy covering. Two of the five nest boxes were glued to the underside of flat-bottomed, concrete bridges (1994); one was glued to the wall of a fish ladder; one was screwed to the inside top of a 3-m-diameter culvert; and one was screwed to the bottom of a stream-spanning log. All structures were >500 m from known nest sites. We recorded nest-site use as we monitored nests during 1993–1995; during 1996–1998, we searched these two reaches at least twice each year and noted only whether the nest sites were in use. We used Analyses of Covariance (PROC GLM; SAS Institute, Inc. 1989) to compare number of active nest sites between Drift and Lobster creeks for the 1993–1998 breeding seasons.

Statistical analyses.—We categorized nest sites into five types, based on their substrate (hereafter referred to as nest type): nest boxes, rock or moss-covered cliff ledges, bridges, cavities or hollows in logs (log cavities), and streambank roots or rootwads. We considered multiple nests in close proximity (<5 m) as representative of one breeding attempt and one active nesting area; within and across years, dippers may build more than one nest at slightly different locations, but will only use one nest (Kingery 1996). We observed no simultaneously active nesting attempts that were closer than 400 m, although others have reported closer nesting (S. A. H. Osborn pers. comm.).

We used logistic regression analysis (PROC LOGISTIC and PROC GENMOD; SAS Institute, Inc. 1989) with a forward variable-selection routine to build models for assessing nest-site selection—specifically (1) to distinguish between bridges used and not used by dippers, and (2) to compare streamside habitat at dipper nests with randomly selected streamside habitat. We used a binary response variable in each model to indicate dipper use (1) versus no use (0). At bridges, the explanatory variables we considered were the length, width, and height of the ledge; the vertical distance to streambed; and the setback distance of the nest. For streamside habitat, we evaluated stream shading, the distance to human activity, valley form, adjacent land use, canopy cover, stream bank vegetation, and riparian zone vegetation. At each step, all variables under consideration were evaluated, and the variable with the greatest explanatory power (greatest reduction in model deviance) was added to the model (i.e., we ran each model changing only the variable of interest and manually calculating the reduction in deviance). We terminated model-building when the additional variable did not improve the model's explanatory power by a drop in deviance ($P \leq 0.10$). We used a liberal significance level for variable entry because more conservative levels often fail to identify important variables (Hosmer and Lemeshow 2000:95). All models met the Hosmer and Lemeshow goodness-of-fit test ($P > 0.050$, Hosmer and Lemeshow 2000). No two variables were highly correlated (all $r < 0.60$, no multicollinearity; Neter et al. 1989); models also met the assumption of linearity (Neter et al. 1989). We tested all first-order interaction combinations (i.e., crossed effects) of the significant variables for each model after the initial variable selection (Neter et al. 1989, Hosmer and Lemeshow 2000). We identified variables that distinguished between (1) microhabitat and macrohabitat at bridges used by dippers versus those not used and (2) streamside habitats where we located nests versus locations that we selected at random. We included three indicator (dummy) variables in all regression models, one for basin and two for stream order, because our objective was to examine habitat selection patterns after accounting for any effects of the two stream basins and three stream orders (Strahler 1957). All odds ratios (Hosmer and Lemeshow 2000:50) from logistic regression analyses are reported relative to a base comparison (i.e., odds ratio = 1). An odds ratio is the multiplicative likelihood of use given a one-unit increase in the value of a given variable. Odds <1 indicate that an increase in the value of that variable decreases the likelihood of use, whereas odds >1 indicate a greater likelihood of use with an incremental increase in the value of that variable.

We used the Mayfield method (Mayfield 1961, 1975) to determine nest survival in each stage of nesting, and program MICROMORT (Heisey and Fuller 1985) to calculate daily survival probabilities and 95% confidence intervals (CI). We report bias-adjusted interval survival rates (Heisey and Fuller 1985). Estimates were based on a 44-day nesting period (19 egg-laying and incubation days, and 25 brood-rearing days); survival was calculated for each stage and the overall period. We calculated survival based on exposure days (total number of days observed). When we observed a nest or brood failure, we used the mid-date between the last visit and the previous visit as the date of failure. Although we did observe nests with unknown causes of failure, we were certain about the fate of each nest (Manolis et al. 2000). We used a *Z*-test (Hensler 1985) to compare observed daily nest survival between the two stream basins, among the five nest types, and between natural and created nest sites. Each nest site hosted one, two, or (rarely) three breeding attempts each season. For each nest site, we calculated the mean and total number of chicks that fledged. We used nonparametric Wilcoxon's rank sum (normal approximation) and Kruskal-Wallis tests (chi-square approximation; Sokal and Rohlf 1981), both conducted with PROC NPAR1WAY (SAS Institute, Inc. 1989) to compare the mean number of chicks fledged between basins and among nest types, respectively. We used Spearman's rank correlation to relate the mean number of chicks produced at each site to 19 measures of microhabitat, macrohabitat, and streamside habitat characteristics: mean and maximum moss thickness on cliffs; length, width, and depth of the nest ledge; length, height, and area of the cliff's vertical surface; height and length of the nest-site cliff; vertical height above and below the nest; verticality of the cliff; diameter of the log associated with log nests; setback distance of the nest; bridge cross-member angle; stream shading; distance to humans; and streamside canopy cover. To control Type I error rates during these simultaneous multiple comparisons, we used the Bonferroni method (Bart and Notz 2005) because of its simplicity and few assumptions. This method guarantees a significance level, α, for M comparisons by adjusting the critical value for each comparison to α/M. We used a paired *t*-test to remove the potential confounding effect of nest-site quality when comparing the number of young fledged from first broods versus second broods. To do this, we calculated the difference in number of young fledged (first brood − second brood) at each site that raised two broods and ran a *t*-test on the difference (H_0: difference = 0). We used SAS (ver. 6.1 and 9.1; SAS Institute, Inc. 1989) to complete all statistical analyses. Values reported are means ± 1 SE.

TABLE 1. Microhabitat and macrohabitat characteristics at American Dipper nest sites on cliff ledges, under bridges, in log cavities, and on roots and rootwads in the Oregon Coast Range, 1994. Uneven sample sizes indicate variables that could not be safely evaluated (e.g., a cliff ledge too high to reach or rootwads in large, unstable debris piles) or would be nonsensical (e.g., ledge dimensions for either enclosed log cavities or nests placed in a tangle of roots) for one or more sites.

	Cliff ledges (n = 20)				Bridges (n = 11)			
	n	Mean	SE	Range	n	Mean	SE	Range
Microhabitat								
Ledge length (cm)	19	185.7	129.1	20–2,500	11	363.0	148.5	10–1,220
Ledge width (cm)	19	22.1	1.8	10–35	11	17.9	1.7	10–31
Ledge to overhang (cm)	19	113.3	39.8	18–∞	11	55.6	8.9	24–110
Macrohabitat								
Cliff height (m)	19	3.8	0.4	2.1–9.0	—[b]	—	—	—
Cliff length (m)	19	20.5	3.7	3–50	—	—	—	—
Cliff verticality[a]	19	94.6	2.3	78–120	—	—	—	—
Cliff vertical area (m^2)	19	44.1	11.6	2–225	—	—	—	—
Height below nest (m)	20	2.4	0.2	1.2–4.4	11	2.7	0.2	1.7–3.8
Setback distance of the nest (m)	20	−0.1	0.1	−1.0–0.3	11	−2.0	0.5	−4.4–0

[a] 90° is exactly vertical, cliffs <90° slope away from the stream, and cliffs >90° slope out over the stream edge.
[b] Parameter not applicable to the substrate type.

RESULTS

We searched 181 km of stream in eight basins in the central Coast Range in 1994 and found 51 active and old nests. Nest densities in individual streams ranged from 1.9 to 3.4 nests/10 km (Loegering 1997). We found 20 nests on cliff ledges, 11 nests under bridges, 17 nests in logs, and 3 nests associated with rootwads. Nests on cliffs were typically placed on rock ledges; however, in three instances, dippers created ledges by selecting a cliff with a thick, mossy mat, slipping behind the moss and pushing it away from the cliff face, thereby creating a space to place a nest. This method of ledge creation has not been described previously and may be limited to areas where moss-covered cliffs are relatively common, such as in the Pacific Northwest. Nests on bridges were placed on horizontal beams or, in many instances, on beams with ledges that sloped downward at a 45° angle, often adjacent to a vertical cross member. Logs that hosted dipper nests generally were within 45° of horizontal, were damaged by flood events, and often had a shattered end or heart-rot that provided a cavity or platform on which a nest could be placed. Roots and rootwads used by dippers as nest sites were either created or exposed by erosion during flood events. We also found 42 sites that were unoccupied but had the best potential for serving as future nest sites.

Microhabitat and macrohabitat.—Dipper nests in the central Oregon Coast Range were typically sheltered from the weather from above (≥85% for all nest types, n = 51), and 100% were placed on a ledge or root. On cliffs, dippers selected ledges that were ≥20 cm long × 10 cm wide (Table 1). We recorded one nest that was placed on a ledge with only 18 cm of overhead clearance between the ledge and a rock overhang (ledge to overhang; Table 1), but most had considerably more clearance. Cliffs ranged considerably in size; however, those used by dippers were vertical or, more often, leaned out over the stream (mean cliff verticality = 95°; Table 1). All nests were safe from terrestrial predators by virtue of height above the streambed or ground and setback distance. Nests in log cavities tended to be closer (lower) to the streambed than other nest types, and all were placed over the stream (Table 1). Most cavity nests were placed in coniferous logs (13/16; tree species was not recorded for one log).

Bridges used by dippers (n = 11) were distinguished from unused bridges (n = 11) by their height and the angle of the cross member in their support structure (logistic regression, χ^2 = 13.2, df = 2, P = 0.001, r^2 = 0.70; Table 2).

TABLE 1. Extended.

Log cavities (n = 17)				Rootwads (n = 3)			
n	Mean	SE	Range	n	Mean	SE	Range
7	36.4	19.5	10–114	1	29.0		
7	29.8	3.7	24–44	1	22.0		
7	115.8	96.1	15–500	2	38.0	10.0	28–48
—	—	—	—	3	3.1	0.9	2.1–4.0
—	—	—	—	2	16.4	8.7	7.7–25.0
—	—	—	—	2	97.5	7.5	90–105
—	—	—	—	2	52.9	47.1	5.9–100
17	1.7	0.1	0.9–3.0	3	1.8	0.1	1.7–2.1
17	−2.3	0.3	−3.8–−0.5	3	−0.1	0.2	−0.4–0.2

Sites on bridges used by dippers were lower (closer to the stream; range = 1.71–3.81 m, n =11) than bridges not used (range = 2.70–8.47 m, n = 10) by dippers (odds ratio = 0.01, 90% CI = 0–0.44; Tables 2, 3), and the probability of dipper use decreased as bridge cross-member angle increased to 90° (odds ratio = 0.83, 90% CI = 0.69–1.0). Overall, bridge cross members supporting nests were set at sharper angles (79.4° ± 5.05, n = 10) than those without nests (85.6° ± 2.08, n = 8); this use pattern was most pronounced on bridges supported by concrete I-beams (bridges supporting nests: 56.7° ± 2.8, n = 3; bridges not used: 84.4° ± 3.1, n = 5).

Streamside habitat selection.—Stream shading, valley form, and the distance to human features distinguished dipper nest sites from other available (unused) locations (logistic regression, χ^2 = 34.4, df = 7, $P < 0.0001$, r^2 = 0.22). Streams at dipper nests were more shaded than the available habitat (58% versus 34%, respectively; Table 4); for each 10% increase in stream shading, the likelihood of dippers selecting that area increased by 1.6 times (90% CI on odds ratio = 1.29–1.85; Table 5). Streams near dipper nests also were constrained by a steep valley wall more often than they were at randomly selected available sites on at least one (91% versus 65% of the observations, respectively) or both (50% versus 20%) sides of the stream. Dipper nests were 3.2 and 9.1 times more likely to occur where the valley walls constrained the stream on one (90% CI on odds ratio = 0.9–11.9) or both sides (90% CI on odds ratio = 2.5–33.9) than in unconstrained reaches (odds ratio = 1; Table 5). Dipper nests were located where trees dominated both sides of the stream (91% of nest locations versus 68% of randomly selected locations; Table 4); however, we were not able to statistically evaluate the importance

TABLE 2. Microhabitat and macrohabitat characteristics distinguishing bridges with (n = 11) and without (n = 11) American Dipper nests in the Oregon Coast Range, 1994. Odds ratio is a multiplicative likelihood of use given a 1-unit increase in the value of a given variable. Odds <1 indicate that an increase in the value of that variable decreases the likelihood of use, whereas odds >1 indicate a greater likelihood of use with an incremental increase in the value of that variable.

Variable	Parameter estimate	SE	Odds ratio (lower, upper 90% CI)
Intercept	29.468	15.124	
Height above streambed	−4.468	2.220	0.01 (0.00, 0.44)
Cross-member angle	−0.183	0.111	0.83 (0.69, 1.00)

TABLE 3. Microhabitat and macrohabitat characteristics of bridges with and without American Dipper nests in the Oregon Coast Range, 1994. The equal sample sizes of used and unused nest sites was coincidental (i.e., these were not paired analyses).

	Used		Unused	
	n	Mean ± SE	*n*	Mean ± SE
Microhabitat				
Ledge length (cm)	11	363.0 ± 148.5	11	486.5 ± 155.1
Ledge width (cm)	11	17.9 ± 1.7	11	14.8 ± 3.3
Ledge to overhang (cm)	11	55.6 ± 8.9	11	47.7 ± 12.6
Macrohabitat				
Vertical distance to streambed (m)	11	2.7 ± 0.2	10	4.6 ± 0.7
Setback distance of the nest (m)	11	−2.0 ± 0.5	8	−2.1 ± 0.6

of riparian forests. Lastly, dipper nests were located farther from human activity (e.g., roads) than unused sites (474 m versus 310 m, respectively). We were 2.5 times more likely to find dipper nests for each additional km away from human activity (90% CI on odds ratio = 1.1–5.7; Table 5), although our farthest nest was only 2.6 km from a road (Table 5).

Productivity.—Reproductive success was markedly high during each nesting stage (*n* = 48 nesting attempts at 16 nest sites over 3 years along Drift and Lobster creeks). Overall daily Mayfield survival of dipper nests was 0.991 (1,219 exposure days, 10 losses, 44-day interval survival = 0.692, 95% CI = 0.556–0.871). Daily Mayfield nest survival during egg laying and

TABLE 4. Streamside habitat (mean ± SE) at American Dipper nest sites and randomly selected locations in Drift and Lobster creeks in the Oregon Coast Range, 1994.

	Known nest sites (*n* = 22)	Randomly selected locations (*n* = 506)
Stream shading (%)	57.7 ± 5.6	34.2 ± 1.3
Distance to human activity (m)	474.0 ± 131.9	309.9 ± 21.2
Riparian zone canopy cover (%)	55.6 ± 3.4	47.3 ± 0.9
Riparian zone trees (%)[a]		
One bank	4.6 ± 4.4	27.3 ± 2.0
Both banks	90.0 ± 6.1	67.8 ± 2.1
Riparian zone conifers (%)		
One bank	36.4 ± 10.3	32.0 ± 2.1
Both banks	18.2 ± 8.2	10.3 ± 1.4
Stream bank trees (%)[a]		
One bank	4.6 ± 4.4	5.9 ± 1.1
Both banks	4.6 ± 4.4	1.4 ± 0.5
Stream bank conifers (%)[a]		
One bank	4.6 ± 4.4	0.2 ± 0.2
Both banks	—[b]	—[b]
Valley form (% constrained)		
One bank	40.9 ± 10.5	44.5 ± 2.2
Both banks	50.5 ± 10.7	20.2 ± 1.8
Land use (% managed forests)		
One bank	0.0 ± 0.0	17.2 ± 1.7
Both banks	81.8 ± 8.2	67.2 ± 2.1

[a] Not included in logistic regression analyses because too few nests were in the response category (i.e., ≤2 nests did not have these features).

[b] All values were zero.

TABLE 5. Riparian habitat variables distinguishing nest sites of American Dippers (n = 22) and randomly located points (n = 506) in the Oregon Coast Range, 1994. We entered indicator variables for basin and stream order into all logistic regression models. Odds ratio is a multiplicative likelihood of use given a 1-unit increase in the value of a given variable. Odds <1 indicate that an increase in the value of that variable decreases the likelihood of use, whereas odds >1 indicate a greater likelihood of use with an incremental increase in the value of that variable.

Variable	Parameter estimate	SE	Odds ratio (lower, upper 90% CI)
Intercept	−5.332	1.052	
Basin 1 (design variable)	−0.470	0.572	0.63 (0.24, 1.60)
Order 4 (design variable)	−2.006	0.928	0.14 (0.03, 0.62)
Order 5 (design variable)	−0.956	0.841	0.39 (0.10, 1.54)
Stream shading (10% increments)	0.435	0.109	1.55 (1.29, 1.85)
Constrained valley form			
One bank	1.159	0.800	3.19 (0.86, 11.87)
Both banks	2.210	0.799	9.11 (2.45, 33.89)
Distance to human activity (km)	0.930	0.487	2.54 (1.14, 5.65)

incubation was ≥0.988 (494.5 exposure days, 6 losses, 19-day interval survival = 0.792, 95% CI = 0.658–0.954). Furthermore, daily nest survival did not differ between Drift (0.990) and Lobster (0.983) creeks (P = 0.52), among nest types (all >0.981, all $P > 0.05$), or between created (1.0) and natural (0.981) nest sites along Drift Creek (P = 0.080). Daily Mayfield survival of chicks was 0.994 (724.5 exposure days, 4 losses, 25-day interval survival = 0.869, 95% CI = 0.760–0.997), and did not differ between Drift (0.996) and Lobster (0.992) creeks (P = 0.56), among nest types (all >0.833, all $P >$ 0.16), or between created (1.0) and natural (0.991) nest sites along Drift Creek (P = 0.16). In 11 attempts, there were no nest or brood failures at created nest sites. Of the 48 nesting attempts for which we had complete histories, ≥1 young hatched in 42 attempts (87.5%) and ≥1 young fledged in 37 attempts (77%). There were no obvious sources of loss for eggs or chicks. All six nests that lost their entire clutch were found empty and undisturbed, and three of the five nests where all chicks were lost showed no signs of disturbance; one nest was disturbed and had a new male in the territory, and one nest contained dead chicks. Neither the mean number of chicks fledged per nesting attempt per site (2.3 ± 0.3, range = 0–4, n = 16 sites; Table 6) nor the total number of chicks fledged per site (mean = 6.75 ± 1.1, range = 0–16, n = 16) was correlated with any of the 19 measurements of microhabitat, macrohabitat, or streamside habitat characteristics (Spearman's rank correlation, all $P > 0.05$; Bonferroni-adjusted critical value for experiment-wise $\alpha = 0.05$: P = 0.003). Mean number of chicks fledged per attempt per site also did not differ between Drift and Lobster creeks (Wilcoxon rank sum, Z = −0.55, df = 15, P = 0.58), among nest types (Kruskal-Wallis, $\chi^2 = 2.5$, df = 4, P = 0.64), or between first and second broods (paired t = −0.52, n = 14, P = 0.61). Overall abundance of nests was 2.7 ± 0.7 nest sites/linear 10 km of stream in 181 km of streams in the Oregon Coast Range (n = 39 streams, mean length = 4.6 ± 1.0 km).

Nest sites in our study were used repeatedly. Between nesting attempts, dippers typically removed and replaced the nest cup but reused the external mossy shell. Of the 12 nest sites we identified in 1993, 8 were used every year for 4 years (otherwise a nearby site within the same territory was active), three sites were idle once during 1993–1996, and one site hosted only a single, failed nesting attempt.

Created nest sites.—By 1996, all created nest sites (n = 9) had been used at least once except for one nest box destroyed by flooding in early 1996. In the year after these sites were created, the number of active nest sites on the experimental reach doubled from three nests to six nests, and the number remained higher on Drift Creek than on Lobster Creek (ANCOVA: $F_{1,10}$ = 6.6, P = 0.029; Fig. 2). This increase represents an increase in the number of dipper breeding pairs, not additional alternate nest sites, because we could uniquely identify one or both

TABLE 6. Apparent reproductive success, total and mean (± SE) number of American Dipper young fledged per attempt per nest site along Drift and Lobster creeks for different nest substrate types, and for first and second broods in the Oregon Coast Range, 1993–1995.

Category	No. nesting attempts observed	No. nests hatching ≥1 egg	No. nests fledging ≥1 chick	Total young fledged	No. sites	No. fledged per attempt per site	*P*
Overall	48	42	37	108	16	2.3 ± 0.32	
Basin							0.58[a]
Drift Creek	29	26	23	68	10	2.5 ± 0.41	
Lobster Creek	19	16	14	40	6	2.1 ± 0.53	
Nest substrate type							0.64[b]
Nest box	3	3	3	9	2	2.9 ± 0.89	
Cliff ledge	20	18	15	42	5	2.2 ± 0.57	
Bridge	18	15	14	42	4	2.5 ± 0.63	
Log cavity	6	5	5	15	4	2.6 ± 0.63	
Rootwad	1	1	0	0	1	0.0 ± 0.00	
Brood							0.61[c]
First	28	26	22	67	14	2.5 ± 0.39	
Second	20	16	15	41	14	2.7 ± 0.34	

[a] Wilcoxon rank sum test (normal approximation).
[b] Kruskal-Wallis (chi-square approximation).
[c] Paired *t*-test.

mates at all nests. Nearly all adult birds (14 of 16) and their young (17 of 23) were uniquely color banded at the nest in the 1st year of the study and 19 more birds were banded after the breeding season; each year thereafter, new birds were banded as they arrived in the study area (140 birds during 1993–1995). Created nest sites were colonized both by new, unbanded immigrants as well as by birds that had previously bred elsewhere within the study basins. Assuming populations were similar in the treated and control reaches prior to the treatment (Drift Creek actually had fewer nests prior to treatment), the increased number of nesting dippers along Drift Creek during all five post-treatment years is indicative of a population response.

DISCUSSION

Habitat selection.—American Dipper nest-site selection was disproportionately influenced by factors at the largest and smallest spatial scales. Given their geographic affinity for un-

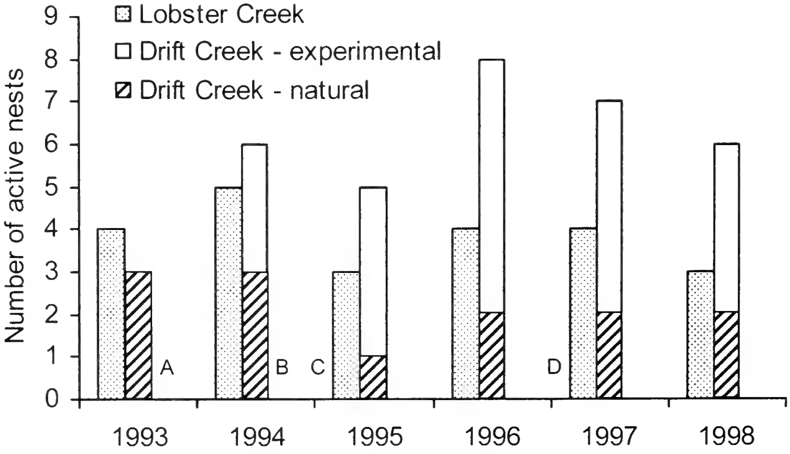

FIG. 2. Number of active American Dipper nests along a portion of Drift and Lobster creeks, Oregon Coast Range, 1993–1998. Seven (A) and two (B) experimental nest sites were constructed after the 1993 and 1994 breeding seasons, respectively, along Drift Creek (9,480-m reach); Lobster Creek (7,800-m reach) was our reference stream. One site was destroyed by flooding prior to the 1995 (C) and 1997 (D) breeding seasons.

polluted, swift mountain streams in western North America (Price and Bock 1983, Kingery 1996), dippers appear to require structures that are large enough to hold a nest, close to the stream, and high enough to reduce destruction from predation or spring flooding. We found no nests that were accessible to terrestrial predators and did not record any nest loss to predators. In contrast, predation was the most important factor in reducing nest success of American Dippers in British Columbia (Morrissey 2004) and White-throated Dippers (*Cinclus cinclus*) in Norway (Efteland and Kyllingstad 1984), suggesting that predation has influenced and continues to influence the evolution of nest-site selection. Moreover, no nests we found were >0.3 m from the stream's edge. Previously, American Dipper nests have been found in trees and shrubs, and farther from the water (Sullivan 1966) than we noted for American Dippers or which Moon (1923), Robson (1956), Balát (1964), and Trochet (1967) noted for White-throated Dippers; however, these are rare occurrences (Price and Bock 1983, this study). Beyond these general requirements, dippers exhibited great flexibility in nest-site selection. Dippers will nest on a diversity of stream sizes and substrates, including on cliff ledges, under bridges, on midstream boulders (Sullivan 1973, Price and Bock 1983), in boxes and log cavities, around rootwads (Hawthorne 1979, Morrissey 2004, this study), and occasionally in gaps in rock walls and bridge drainpipes (Everett and Marti 1979). A comprehensive study of nest characteristics of White-throated Dippers in Europe yielded similar results (Shaw 1978).

Streamside habitat at dipper nests differed from that available, which may reflect microhabitat and macrohabitat selection. Geomorphically constrained valleys have steeper slopes, more cliffs, and a greater potential for microhabitats that are suitable for nesting (e.g., ledges) than unconstrained valleys. Most dipper nest sites were located where trees dominated the adjacent riparian zone on both sides of the stream, and nest sites were located where the stream was more heavily shaded by those trees. The importance of streamside forests extends beyond the observed pattern. Riparian-zone trees contribute large logs to the stream and stream bank (Meehan et al. 1977, Swanson and Lienkaemper 1978, Keller and Swanson 1979, Sedell et al. 1988). Logs from mature hardwoods and conifers not only add wood to the stream and increase its structural complexity, but also may provide nest sites. To a large extent, future nest-site availability may depend on there being a conifer component in riparian areas; ≥80% of the nests that we found in log cavities were in coniferous logs, yet in only 42% of the basins were conifers the dominant trees on either side of the stream. Moreover, 32% of the nests we found were placed on or in large dead wood; however, nests associated with large wood or logs are listed as only occasional (0–5% of observed nests) or are not mentioned at all in previous reviews (Ealey 1977, Kingery 1996).

We have revealed at least three lines of evidence that suitable nest sites for dippers may be in short supply. First, during our surveys, only 1 of 42 sites that we identified as possible nest sites—but with no evidence of past use—met minimal criteria that we derived from the literature (Price and Bock 1983, Kingery 1996). Twenty-eight (67%, $n = 42$) of these sites failed to meet the minimal requirements of a platform or ledge ≥10 × 10 cm, inaccessibility to terrestrial predators, being >1 m above the streambed, and (for bridges) having a cross-member angle of <80°. Eight suitable nest sites (19%) were <500 m from a dipper nest and likely within the same territory (see Ealey 1977, Price and Bock 1983, this study). Of the remaining six (14%) unused sites, three were ≥1.2 m from the water, and two sites were subjectively classified as "poor" sites. Second, sites that were used were occupied nearly every year. Third, the use of created nest sites further corroborated the possibility that nest sites are limited. All created structures were colonized within 2 years of their creation, except for one that was destroyed by flooding before it could be used. This more than doubled the number of active nests on Drift Creek from 1993 to 1996. Overall, the lack of suitable but unused sites, the high re-occupancy rate, and the rapid colonization of created sites indicates that suitable nest sites may have limited the abundance of dippers in our study basins. However, there may be regional variation, as Feck and Hall (2004) found several unoccupied sites in Wyoming and concluded that macroinvertebrate prey strongly affected dipper breeding presence in their study area.

Productivity.—Reproductive success was not correlated with any feature of nest-site habitat at the microhabitat, macrohabitat, or streamside scales. Productivity and survival were high and did not differ among nest sites or nest types. Similarly, Feck and Hall (2004) found that productivity was unrelated to any of the physical or biological variables they considered. Conversely, Price and Bock (1983) found nest and fledging success positively correlated with an index of nest-site quality. We did not detect any reproductive advantage attributable to differences in nest-site characteristics for the 16 nest sites in our study; once the minimum criteria for suitability were met, nests were generally successful. The number of chicks fledged per attempt in Oregon was greater and less variable than that reported in Colorado (Price and Bock 1983), Montana (Bakus 1959, Sullivan 1973), Wyoming (Feck and Hall 2004), Alberta (Ealey 1977), or Europe (Balát 1964), but lower than what was reported in British Columbia (Morrissey 2004). In our study, the abundance of breeding American Dippers was lower than it was in British Columbia (Morrissey 2004), Colorado (Price and Bock 1983), or Alberta (Ealey 1977); however, both Sullivan (1973) and Osborn (1999) found nest densities in Montana (0.3 nests/km) that were comparable to ours (0.3 nests/km) and noted that the majority of nests found were under bridges. Suitable nest sites appear to limit the breeding population elsewhere (e.g., Price and Bock 1983, Fite 1984, Kingery 1996, Osborn 1999).

Minimum nest-site requirements.—Based on the relatively high levels of productivity, dippers appeared to select nest sites that met minimal requirements for a site to be suitable for successful reproduction, specifically (1) an adequate ledge or physical space for a nest, (2) close proximity to the stream's edge, (3) safety from terrestrial predators, and (4) a low chance of spring flooding. The presence of an adequate ledge seems obvious, but not all cliffs offer suitable nesting space. The smallest log cavity used was 13 cm in height, width, and depth. Suitable ledges also should exceed 13 cm and be larger if the ledge is not horizontal. Nests can be inaccessible to ground predators because of the elevation of the nest ledge and/or the distance from the stream's edge. Every dipper nest we located ($n = 51$) was over the stream or its edge (>77% had ≤0 m setback distance), or was within 0.3 m of the stream's edge (<23%); this was also the case in the Oregon Cascades ($n = 30$, Loegering 1997). Further inaccessibility may be afforded on high ledges associated with near-vertical cliffs. Bridges have this obvious advantage; however, not all have suitable ledges for nest placement. Bridges constructed of used railroad flatcars provide excellent nest sites if the ledges do not extend to the abutments, thus allowing mammalian access. Bridges with concrete, I-style beams provide suitable nest sites, but only if the central cross member between the parallel supports is placed at an acute angle (≤60°), permitting dippers to wedge their nest against the walls of the support and cross member. Interestingly, dippers in Utah and Montana nested successfully by nesting under bridges without cross members (R. E. Donnelly and S. A. H. Osborn pers. comm.). By virtue of their position over the stream, log cavities are even more protected from predators. Sufficient diameter is needed for logs to develop cavities large enough to hold a nest. We found nests in logs that were 40–150 cm in diameter; however, a 31-cm-diameter branch overhanging the stream contained a nest cavity that was created when the majority of the branch was ripped off by a windstorm or spring flood.

Management implications.—Breeding dipper populations in the Oregon Coast Range appear to be limited by the availability of suitable nesting substrates. Suitable dipper nest sites, and consequently recruitment from those sites, are dependent on the physical characteristics of the nest-site. However, suitable sites are not abundant and are mostly products of geomorphology and human development (i.e., bridges). If warranted, effective options to increase breeding abundance include providing nest boxes, creating ledges and cavities, and modifying existing structures (e.g., bridges) to provide suitable nest sites. A long-term, natural alternative for nest-site recruitment may be the conservation of large coniferous logs in riparian systems. Timber harvest operations that reduce the amount of large wood along streams should be avoided, and managers should protect and encourage conifer-dominated riparian areas. Large logs that fall into the stream channel and along the stream bank from riparian areas or the upslopes (Swanson et al. 1976, Van Sickle and Gregory 1990, Fetherston et al. 1995) can contribute to heterogeneity in the channel and riparian zone (Keller and Swanson 1979, Bilby 1988, Gregory et al. 1991) and potentially serve as nest or foraging sites (S. A. H. Osborn pers. comm.) for dippers.

Coniferous logs also have greater longevity than comparably sized red alder logs (Swanson and Lienkaemper 1978), and they have the potential to reach a larger diameter, further increasing their persistence as nest sites or structural components of riparian systems. Current guidelines for private and state forests (Oregon Forest Practices Act 1994) that require maintenance of the community structure and specific conifer stocking levels in riparian areas appear to be adequate. Overall, resources needed by dippers should be adequately protected by the guidelines for federal forests (Forest Ecosystem Management Assessment Team 1993), which limit disturbance in riparian areas. Unfortunately, our sampling of riparian habitat extended only 25 m from the stream's edge and did not allow us to evaluate differing buffer widths in riparian zones. Subsequent research should address this concern.

ACKNOWLEDGMENTS

The Coastal Oregon Productivity Enhancement Program and the U.S. Bureau of Land Management funded this study. The Oregon Cooperative Fish and Wildlife Research Unit provided financial and technical support throughout the entire project. We are grateful to N. V. Marr, L. L. Loegering, and K. Popper for field assistance. Earlier drafts of this manuscript were greatly improved by comments from K. G. Beal, R. E. Donnelly, H. E. Kingery, S. A. H. Osborn, and two anonymous reviewers. Methods and techniques used to capture and handle dippers were approved by Oregon State University's Institutional Animal Care and Use Committee.

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The Wilson Journal of Ornithology 118(3):295–308, 2006

UPLAND BIRD COMMUNITIES ON SANTO, VANUATU, SOUTHWEST PACIFIC

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ABSTRACT.—We surveyed indigenous landbirds at two upland, mostly forested sites in southwestern Santo, Vanuatu. One site (Wunarohaehare, 600–1,250 m elevation) lies on the western, rain-shadowed slope of Mt. Tabwemasana. The other (Tsaraepae, 500–700 m elevation) is 16 km to the south, on the southeastern, very wet slope of Peak Santo. These are the richest single-site bird communities yet surveyed in Vanuatu, with 30 species of resident birds recorded at each site, 27 of which were common to both sites, including 6 species endemic to Vanuatu. We judged that 12 of the shared species were common at both sites. The non-overlapping species were a megapode, a parrot, and four understory passerines. We present new data on vocalizations for four species endemic to Vanuatu (*Ptilinopus tannensis*, *Todiramphus farquhari*, *Neolalage banksiana*) or to Vanuatu plus New Caledonia (*Clytorhynchus pachycephaloides*). We found less seasonality in breeding than previously reported for Vanuatu. Most human impact at the sites today may be from non-native mammals (rats, cats, pigs, cows), along with low levels of hunting and forest clearing. Based on prehistoric bones from elsewhere in Vanuatu, we suspect that formerly the sites on Santo may have supported additional species of megapode, hawk, parrot, and starling. *Received 28 July 2005, accepted 14 March 2006.*

The Republic of Vanuatu (12,195 km^2; Fig. 1) consists of 12 islands >270 km^2 and nearly 100 smaller ones in the tropical Pacific Ocean. Approximately 190,000 persons inhabit 70 islands (Lal and Fortune 2000) that range from active volcanoes to limestone islands to older, geologically composite islands, such as Santo (MacFarlane et al. 1988, Nunn 1994). Analyses of avian distributions in Vanuatu, based largely on collections made during the Whitney South Sea Expedition on 31 islands in 1926 and 1927 (e.g., Mayr 1934, 1941), have been important in the development of evolutionary theory (Mayr 1963) and the fields of island biogeography (MacArthur and Wilson 1967) and community ecology (Diamond 1975). Aside from the study by Scott (1946), field ornithology in Vanuatu lagged until the Percy Sladen expedition of 1971 focused on inter-island and altitudinal patterns of avian distribution across six islands in the archipelago (Medway and Marshall 1975). Despite the continued interest by ecologists in the results of surveys conducted decades ago (e.g., Sanderson et al. 1998, Gotelli and Entsminger 2001), little recent attention has been paid to gathering new data on intra- and inter-island variation in Vanuatu's bird communities (although see Bowen 1997). Bregulla (1992) summarized information on identification, life-history, and distribution for each species recorded from the island group, yet made it clear that much remains to be learned about the basic biology of Vanuatu's birds. Although most biogeographic analyses of insular faunas (or floras) are based on lists of species from an entire island, such lists typically contain species that seldom, if ever, interact because they are not syntopic. Especially on large islands such as Santo, the sets of species found at single sites provide fertile grounds for analysis.

In 2002 and 2003, we made two trips to Santo, Vanuatu's largest (3,900 km^2) and highest (1,879 m) island, home to eight of the nine bird species endemic to the archipelago (Bregulla 1992). We surveyed birds at two mid-elevation rainforest sites, one each on the southeastern (windward) and western (leeward) slopes of Santo's rugged west-coast mountain range. Our surveys were based on sight/sound records, mist netting, tape-recordings, and specimens collected: skins with wings spread, skeletons, tissues, stomach contents, and ectoparasites from the same indi-

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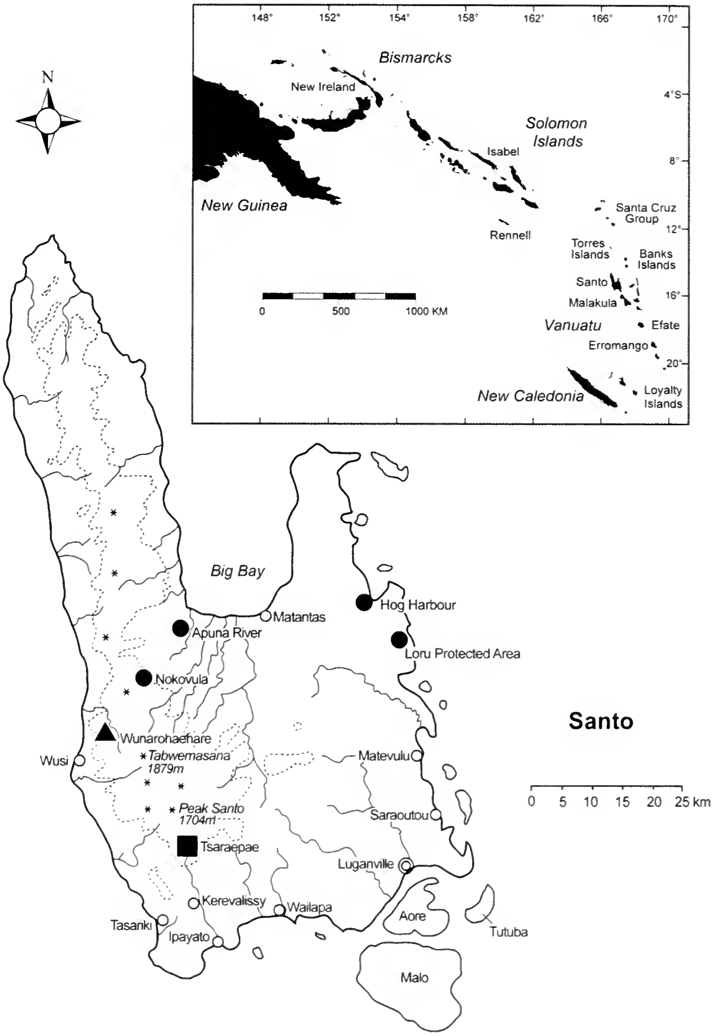

FIG. 1. Map of Espiritu Santo, Vanuatu, with an inset of Melanesia. Islands and island groups mentioned in the text are named. Sites of bird surveys conducted from 2002–2003 by the authors are indicated by the triangle (Wunarohaehare) and the square (Tsaraepae), and filled circles indicate sites surveyed by Bowen (1997; Loru Protected Area) and Medway and Marshall (1975; Nokovula, Apuna River, Hog Harbour). Asterisks = mountain peaks >1,400 m; dashed line = 600-m contour.

vidual, along with data on habitat, molt, diet, and reproductive condition. Such information is a first step in the investigation of ecological, morphological, and genetic differences among populations, and it is important for conservation efforts that often focus on endemic taxa.

In this paper, we present the results of our surveys at each site, focusing on Vanuatu's endemic and poorly known species. We also present comparisons with previous surveys at sites elsewhere on Santo and in the Solomon Islands.

METHODS

The island of Espiritu Santo (generally called Santo; Fig. 1) probably originated in the Oligocene (ca. 25–30 mya) through volcanism and tectonic uplift, although most of its land formed during or since the Miocene through these same processes (Mallick 1975, Collot and Fisher 1989). Much of the island's eastern half is flat or has rolling hills, with most land <300 m in elevation and very little of it above 600 m. The western half of Santo is dominated by a north-south trending moun-

TABLE 1. Study sites and mist-netting effort on Santo, Vanuatu, 2002–2003.

Site (latitude, longitude)	Major habitats	Netting dates	Elevation (m)	No. nets	Net-hr
Wusi village (15° 22.7′ S, 166° 39.7′ E)	Dry lowland forest, secondary scrub	22–27 Oct 2002, 4–5 Nov 2002	0–50	8	165
Wunarohaehare[a] (15° 20.5′ S, 166° 40.5′ E)	Humid premontane forest, forest patches, grassy ridge	29 Oct–2 Nov 2002	600–1200	18	337
Kerevalissy village (15° 35.7′ S, 166° 50.0′ E)	Secondary lowland forest patches	3–6 and 14 Jun 2003	200	5	14
Tsaraepae[a] (15° 32.7′ S, 166° 48.4′ E)	Wet, primary, premontane forest	7–14 Jun 2003	500–700	15	575

[a] Primary study sites.

tain range that reaches its greatest height at Mt. Tabwemasana (1,879 m). Prevailing winds push moist air off the Pacific Ocean across the eastern lowlands and into the east- or southeast-facing slopes of the main cordillera. Thus, the eastern and southern slopes of the cordillera are humid with high precipitation, whereas the western slopes, which plunge into the Pacific with little development of a coastal plain, lie in a rain shadow and are relatively dry.

From 22 October to 5 November 2002, we (AWK, JJK) mist-netted and observed birds in dry forest and scrub in the vicinity of Wusi (Fig. 1, Table 1), a village in the rain shadow on the western coast 10 km west of Mt. Tabwemasana, and in humid premontane forests and grassy ridges from 600 to 1,250 m elevation on the northern slope of Mt. Wunarohaehare (denoted by a triangle in Fig. 1; Table 1). At Wunarohaehare, figs (*Ficus* spp.) and nutmegs (*Myristica* spp.) are the dominant fruiting trees. Tree ferns (*Cyathea* spp., *Dicksonia* spp.) become common above 700 m in a transitional habitat between the "high-stature lowland rain forest" and the "montane cloud forest" (described in Mueller-Dombois and Fosberg 1998). The weather at Wunarohaehare is cool and moist in the morning, as cloud cover descends below 600 m. By 10:00 UTC + 11, however, the clouds dissipate and the canopy receives direct sunlight. Short periods (<1 hr) of rain occur most afternoons.

From 3 to 14 June 2003, AWK, JJK, and DWS worked on the southern slopes of Peak Santo (also called Lairiri; 1,704 m), ~16 km south-southeast of Mt. Tabwemasana. This area received the full precipitative effects of moist air coming off the Pacific, and was much wetter than sites in the rain shadow—Wusi and Wunarohaehare. From 3 to 7 June, we surveyed a patchy secondary forest near Kerevalissy village (Fig. 1, Table 1), a landscape dominated by coconut plantations, ~4 km north of the coastal village of Ipayato. From 7 to 14 June, we mist-netted (Table 1) and observed birds on the southern slopes of Peak Santo at Tsaraepae (~500 m; denoted by the square in Fig. 1) and on nearby slopes up to 700 m elevation. Ridges in the lower elevations had a broken canopy and were cleared of undergrowth, grazed by feral cattle (*Bos taurus*), and browsed by feral pigs (*Sus scrofa*). The area >700 m was mainly tall (canopy 12–25 m) forest.

Trees identified (by DWS) to genus included *Garuga* (Burseraceae), *Calophyllum* (Clusiaceae), *Elaeocarpus* (Elaeocarpaceae), *Hernandia* (Hernandiaceae), *Ficus* (Moraceae; at least five species, some of them emergent), and *Myristica* (Myristicaceae); those we identified to species included *Barringtonia edulis* (Barringtoniaceae) and *Endospermum medullosum* (Euphorbiaceae; often emergent). There also were a number of unknown species, including various Myrtaceae and Rubiaceae. Also present were *Pandanus* spp. (Pandanaceae), tree-ferns (*Cyathea* spp.; Cyatheaceae), and *Dicksonia* spp. (Dicksoniaceae). The edges included trees and shrubs of *Macaranga* spp. (Euphorbiaceae), *Inocarpus fagifer* (Fabaceae), *Ficus* spp., *Piper* spp. (Piperaceae), *Alphitonia* spp. (Rhamnaceae), *Pipturus* spp. (Urticaceae), palms (*Cocos* spp.; *Metroxylon* spp. [Arecaceae]), and thickets of *Hibiscus tiliaceus* (Malvaceae), bananas (Musaceae), and gingers (Zingiberaceae).

The weather at Kerevalissy and Tsaraepae in 2003 was extremely wet, with heavy rainfall occurring on 11 of our 12 days. On 9 days we estimated that the daily rainfall exceeded 100 mm, including 6 days (5, 6, 8, 9, 12, and 13 June) on which it probably exceeded 150 mm. The excessive rain was due to an unusually late tropical storm that paused just north of Santo over the Banks and Torres islands. Because avian activity did not diminish noticeably during rains at Tsaraepae, we conducted our sight/sound surveys and set mist nets even during the very rainy weather. Vocalizations were tape-recorded on several days at each of our two primary sites (Table 1), and the original tapes were deposited in the Florida Museum of Natural History (UF) Sound Archives. Birds were collected according to the stipulations of our permits from the Vanuatu Ministry of Lands, Environment Unit. Specimens were prepared as various combinations of round skins, complete or partial skeletons, and with spread wings. Stomach contents and two tissue samples were taken from each specimen; one tissue sample is housed at UF and the other at the Louisiana State University Museum of Natural Science. All non-tissue material is housed at UF. As far as we know, neither tissue nor skeletal specimens of birds had been collected previously in Vanuatu. The skeletal specimens of the Vanuatu endemics *Ducula bakeri*, *Ptilinopus tannensis*, *Todiramphus farquhari*, *Neolalage banksiana*, *Zosterops flavifrons*, and *Glycifohia notabilis* (see Tables 2 and 3 for English common names) are the first in the world's inventories.

In addition to our work at the two primary sites, JJK and AWK collected and surveyed birds in patchy forested sites near sea level on the eastern coast of Santo for 2 days in October–November 2002 and for 4 days in June 2003. In northern Santo, AWK visited lowland forests of the Vatte Conservation Area (near Matantas; Fig. 1) from 17 to 19 November 2002. DWS visited Aore Island (Fig. 1) on 15–16 June 2003, surveying (sight/sound only) birds in patches of tall (canopy 15–30 m) lowland rainforest.

Although this was the first visit to Santo by all three authors, AWK and especially DWS have wide experience with the avifauna in western Oceania. They know the vocalizations and behaviors of all but one of the genera found on Santo. Nonetheless, cryptic species may have been missed if they were not vocal during our visits.

RESULTS

Diversity and community composition.—We recorded 33 indigenous species of landbirds at Wunarohaehare and Tsaraepae, with 27 species common to both sites (Table 2). As is the case across most of Oceania (Steadman 1997, 2006b), pigeons and doves (Columbidae) composed a large part of the avifauna; the same seven species of columbids were found at each site. We also recorded seven of the eight species endemic to Vanuatu, failing to record only *Aplonis santovestris* (see below). Six of the endemic species (all but *Megapodius layardi*) were recorded at both sites.

Although three species of non-native birds are widespread on Santo (Red Junglefowl, *Gallus gallus*; Common Myna, *Acridotheres tristis*; and Black-headed Munia, *Lonchura malacca*), the only one we recorded was *G. gallus*, and it was uncommon (<5/day) at both sites. All three species were common in plantations and villages at elevations lower than those of Wunarohaehare and Tsaraepae. Contamination of the bird communities by non-native species on Santo is minor (by Pacific Island standards); however, both sites are heavily infested with non-native mammals. At Tsaraepae, we noted feral cats (*Felis catus*), pigs (*Sus scrofa*), and cows (*Bos taurus*); dogs (*Canis familiaris*) seemed to be confined to villages. Inside our leaf house at Tsaraepae, DWS snap-trapped 10 rats (7 *Rattus rattus*, 3 *R. exulans*) in 3 nights, using only two traps.

Although species richness was the same at our two primary sites, composition of the landbird communities differed slightly. *Megapodius layardi*, *Charmosyna palmarum*, and *Clytorhynchus pachycephaloides* were found only at Tsaraepae, although the latter species was found in the dry forests near Wusi (lower elevations than at Wunarohaehare). The mound-building *Megapodius layardi* may be absent from dry forests due to unsuitable soil conditions. Our failure to record *Charmosyna palmarum* at Wunarohaehare may have been a consequence of its nomadic habits (see *C. palmarum* species account, below). Three species with widespread distributions in Oceania—*Lalage leucopyga*, *Turdus polioce-*

phalus, and *Petroica multicolor*—were not recorded at Tsaraepae. The four passerine species found at only one of the two sites have been recorded on both sides of the cordillera (Medway and Marshall 1975; Table 3), so their apparent absence at one site may be related to inadequate sampling. We note, however, that our guides at Tsaraepae did not recognize the illustration in Bregulla (1992) of *Turdus poliocephalus*, suggesting that the local absence of this conspicuous species was genuine. The guides did not distinguish between *L. maculosa* and *L. leucopyga* (Hakei language names for *Lalage* were "vasoimoto" and "losoloso," which seemed to apply to either species), so it is possible that the latter species was present. Our guides did know *Petroica multicolor*, however, and called it "panopano."

We observed inter-site differences in the altitudinal ranges of some species. Two endemic species characteristic of the highlands (*Ducula bakeri* and *Glycifohia notabilis*) were more common at Tsaraepae than at Wunarohaehare, where *D. bakeri* was not seen below 800 m. At Tsaraepae, *D. bakeri* was found regularly as low as 500 m and locally in forest patches as low as 200 m along the trail south toward the coast. At Tsaraepae, the fantail, *Rhipidura spilodera*, was scarce above 500 m, but at Wunarohaehare it was common up to 800 m. Some species associated with less forested habitats (*Todiramphus chloris*, *Lalage maculosa*, *Gerygone flavolateralis*) were found at higher elevations at Wunarohaehare, where we sampled open habitats up to 1,000+ m; at Tsaraepae, however, we did not find these species at elevations above 550 m, which were almost entirely forested.

Seasonality of reproduction.—Our visit to Wunarohaehare during October–November coincided with the reported breeding period for most species of birds in Vanuatu, which generally is September–February (Bregulla 1992). Our visit to Tsaraepae took place during June, a month when Bregulla (1992) found breeding activity for only 5 of the 33 species we recorded (Table 2). We found less evidence of marked seasonality in breeding, with signs of reproductive activity (enlarged gonads in specimens, active nests, or recently fledged juveniles) in 20 of 23 species at Wunarohaehare and 12 of 20 species at Tsaraepae (Table 4). We suspect, nevertheless, that the difference between the two sites (87% versus 60% of species) does reflect seasonal trends more than inter-site variation.

Selected Species Accounts

We present our findings for species endemic to Vanuatu and for some others that are poorly known in Vanuatu or throughout their range.

Megapodius layardi.—The endemic Vanuatu Megapode was not recorded at Wunarohaehare, but, at Tsaraepae on 11 and 12 June, three individuals were heard calling at an elevation of 550 m in the thick undergrowth near an active incubation mound in a large tract of forest. This was the only mound near Tsaraepae known to our guides. Another bird was observed in a dense *Hibiscus tiliaceus* thicket at 600 m on 11 June. Single birds also were seen twice in secondary forest patches on Santo's eastern coast, and once near Matantas. Villagers showed us eggs from an active mound near Matevulu on 16 June.

Chalcophaps indica.—This terrestrial dove is widespread in Oceania, with the subspecies *C. i. sandwichensis* confined to New Caledonia, the Santa Cruz Group, and Vanuatu. Abundant in disturbed forest and forest edge from sea level to 400 m elevation (lower than either study site), the Emerald Dove was much less common in more mature forest near our two primary study sites. In 337 net-hr at Wunarohaehare, only one bird was netted at elevations >500 m, whereas five were netted in 165 net-hr at 0–50 m near Wusi. Because it seldom vocalizes and is rather furtive, mist-netting may yield better evidence of the Emerald Dove's population density than auditory or visual data. The species is common in village gardens, where it often is lured with papaya (*Carica papaya*) into traps; stomachs of nearly all collected individuals contained seeds of this non-native plant. The four birds taken near Wusi village included two males with enlarged testes, an adult male (no bursa) with unenlarged testes, and an adult female (no bursa, convoluted oviduct) with slightly enlarged ova. The single bird from Tsaraepae was a male with enlarged testes.

Ptilinopus tannensis.—Endemic to Vanuatu, the Tanna Fruit Dove was common (up to 15 per day) at each site, especially in montane forests. This fruit dove was heard much more

TABLE 2. Summary of native bird communities at two sites (Wunarohaehare, 600–1,200 m; Tsaraepae, 500–700 m) on Santo, Vanuatu, surveyed in 2002–2003. E = endemic to Vanuatu, e = endemic to Vanuatu plus New Caledonia and/or the Santa Cruz Group. Relative abundance: c = common (encountered regularly by all observers), u = uncommon (encountered daily or almost daily in small numbers), r = rare (encountered fewer than five times), — = not recorded. Foraging guild (microhabitat/prey): A = aerial, C = canopy, T = terrestrial, U = understory, F = fruit, G = granivore (seeds), I = insects and other invertebrates, N = nectar, V = vertebrates. Avian nomenclature follows Dickinson (2003), except that we do not recognize *Aerodramus*, which has been used for some species in *Collocalia* (but see Price et al. 2004).

Species	Relative abundance		Foraging guild
	Wunarohaehare	Tsaraepae	
Megapodiidae			
Megapodius layardi, Vanuatu Megapode (E)	—	r	T/F,G,I
Accipitridae			
Circus approximans, Swamp Harrier	r	r	A/V
Columbidae			
Columba vitiensis leopoldi, White-throated Pigeon	r	u	T,U,C/F,G
Macropygia m. mackinlayi, Mackinlay's Cuckoo-Dove	c	u	U/F
Chalcophaps indica sandwichensis, Emerald Dove	c	c	T/G,I,F
Ptilinopus tannensis, Tanna Fruit Dove (E)	c	c	C/F
Ptilinopus greyii, Red-bellied Fruit Dove (e)	c	c	U,C/F
Ducula p. pacifica, Pacific Imperial Pigeon	c	c	C/F
Ducula bakeri, Vanuatu Imperial Pigeon (E)	u	c	C/F
Psittacidae			
Trichoglossus haematodus massena, Rainbow Lorikeet	c	c	C/N,F
Charmosyna palmarum, Palm Lorikeet (e)	—	r	C/N
Cuculidae			
Chrysococcyx lucidus layardi, Shining Bronze-Cuckoo	u	r	C/I?
Apodidae			
Collocalia esculenta uropygialis, Glossy Swiftlet	c	c	A/I
Collocalia v. vanikorensis, Uniform Swiftlet	c	c	A/I
Alcedinidae			
Todiramphus farquhari, Chestnut-bellied Kingfisher (E)	u	c	U/I,V
Todiramphus chloris santoensis, Collared Kingfisher	u	u	C/I,V
Meliphagidae			
Glycifohia n. notabilis, White-bellied Honeyeater (E)	u	u	C/N,I
Myzomela cardinalis tenuis, Cardinal Honeyeater	c	c	C/N,I
Acanthizidae			
Gerygone flavolateralis correiae, Fan-tailed Gerygone	u	u	U,C/I
Artamidae			
Artamus leucorhynchus tenuis, White-breasted Woodswallow	u	u	A/I
Campephagidae			
Coracina caledonica thilenii, Melanesian Cuckoo-shrike	u	u	U,C/F,I
Lalage maculosa modesta, Polynesian Triller	u	r	U,C/F,I
Lalage leucopyga albiloris, Long-tailed Triller	u	—	U/F,I
Pachycephalidae			
Pachycephala [*pectoralis*] *caledonica intacta*, New Caledonian Whistler (e)	c	c	U/I
Petroicidae			
Petroica multicolor ambrynensis, Pacific Robin	u	—	U,C/F,I
Rhipiduridae			
Rhipidura [*fuliginosa*] *albiscapa brenchleyi*, Gray Fantail	r	u	U/I
Rhipidura s. spilodera, Streaked Fantail	c	u	T,U/I

TABLE 2. Continued.

Species	Relative abundance		Foraging guild
	Wunarohaehare	Tsaraepae	
Monarchidae			
Neolalage banksiana, Buff-bellied Monarch (E)	c	c	U/I
Clytorhynchus pachycephaloides grisescens, Southern Shrikebill (e)	—	u	U/I
Myiagra caledonica marinae, Melanesian Flycatcher	c	c	U,C/I
Zosteropidae			
Zosterops flavifrons brevicauda, Yellow-fronted White-eye (E)	c	c	U,C/N,F,I
Zosterops lateralis tropicus, Silver-eye	c	c	U,C/N,F,I
Turdidae			
Turdus poliocephalus vanikorensis, Island Thrush	c	—	T,U/F,I

often than seen, although it called less frequently than the Red-bellied Fruit Dove. Contrary to Medway and Marshall (1975) and Bowen (1997), we found the Tanna Fruit Dove above 500 m; it remained common up to the highest continuous forests that we reached at both Wunarohaehare (800 m) and Tsaraepae (700 m). The most common call was a series (~10+) of low, upwardly inflecting *woot* notes, spaced up to 2 sec apart. Infrequently, it also gave a soft, single *woot* note.

We found the Tanna Fruit Dove breeding at both sites. Bregulla (1992) reported its nesting status as poorly known, with previous evidence reported only in April and May, a time of little breeding activity among other landbirds in Vanuatu. At Wunarohaehare, a nearly fledged nestling was found on the ground after a windy evening, and two males had enlarged testes and a female had enlarged ova. At Tsaraepae, the one bird collected was a female with enlarged ova.

Ptilinopus greyii.—The monotypic Red-bellied Fruit Dove is confined to New Caledonia, the Loyalty Islands, and Vanuatu. The species was abundant (≤50/day) at both sites in heavily disturbed to mature forests and at all elevations. It vocalized throughout the day. All specimens showed evidence of breeding: at Wunarohaehare, these included a female with a ruptured follicle, another with enlarged ova, a male with enlarged testes, and a recently fledged juvenile; at Tsaraepae, the specimens included two males with enlarged testes, a female with enlarged ova, and two juveniles.

Ducula bakeri.—The monotypic Vanuatu Imperial Pigeon is endemic to seven islands in northern Vanuatu. Although rare or absent in the lowlands of Santo, it was common at Tsaraepae, where two or three calling individuals often were audible from many points on a forested ridge at ~600 m, and we recorded as many as 20 on single days. It was less common on the disturbed slopes below 500 m, although we heard it in a forest patch adjacent to Kerevalissy on 14 June. At Wunarohaehare, we found the Vanutau Imperial Pigeon only at elevations >800 m, where up to three individuals called in heavy forest cover on most days. The birds taken at Tsaraepae were an adult female with enlarged ova and a juvenile male. They differed little in plumage, and both had *Myristica* spp. fruits in their crops and stomachs.

Charmosyna palmarum.—The monotypic Palm Lorikeet is endemic to Vanuatu and the Santa Cruz Group. We recorded this species only twice (a flock of six on 8 June, a group of two on 11 June), both times in a *Ficus* spp. tree with large, fleshy fruits, in humid forest at 650 m on the main ridge at Tsaraepae. Although more characteristic of montane than lowland habitats, the Palm Lorikeet seems to undergo population fluctuations and has a propensity to wander (Medway and Marshall 1975, Bregulla 1992). Its preferred foods (flowers and fruits) may have been scarce at the time of our visits.

Collocalia esculenta uropygialis and C. v. vanikorensis.—Each of these widespread swiftlets was common at Tsaraepae. The Glossy Swiftlet (*C. esculenta uropygialis*; 20–

TABLE 3. Indigenous birds recorded (+ = present, − = not recorded) at six sites on Santo, Vanuatu, 2002–2003. English common names are provided for the species not included in Table 2. E = endemic to Vanuatu, e = endemic to Vanuatu plus New Caledonia and/or the Santa Cruz Group. Sources are Bowen (1997) for Loru Protected Area; Medway and Marshall (1975) for Apuna River, Hog Harbor, and Nokovula; and our own data for Wunarohaehare and Tsaraepae. For each site, the elevation (m) is included.

Species	Loru Protected Area 0–120 m	Apuna River 100 m	Hog Harbor 160 m	Wunarohaehare 600–1,250 m	Tsaraepae 500–700 m	Nokovula 1,120 m
Megapodius layardi (E)	+	+	−	−	+	−
Falco peregrinus, Peregrine Falcon	+	−	−	−	−	+
Circus approximans	+	+	−	+	+	+
Gallirallus philippensis, Banded Rail	+	−	−	−	−	−
Columba vitiensis	+	+	−	+	+	−
Macropygia mackinlayi	+	+	+	+	+	+
Chalcophaps indica	+	+	+	+	+	+
Ptilinopus tannensis (E)	+	+	−	+	+	−
Ptilinopus greyii (e)	+	+	+	+	+	+
Ducula pacifica	+	+	+	+	+	−
Ducula bakeri (E)	−	−	−	+	+	+
Trichoglossus haematodus	+	+	+	+	+	−
Charmosyna palmarum (e)	−	−	−	−	+	+
Chrysococcyx lucidus	−	−	−	+	+	−
Tyto alba, Barn Owl	+	−	−	−	−	−
Collocalia esculenta uropygialis	+	+	−	+	+	+
Collocalia v. vanikorensis	−	+	−	+	+	−
Todiramphus farquhari (E)	+	+	+	+	+	−
Todiramphus chloris	+	−	−	+	+	−
Glycifohia n. notabilis (E)	−	−	−	+	+	+
Myzomela cardinalis	−	+	+	+	+	+
Gerygone flavolateralis	−	+	+	+	+	+
Artamus leucorhynchus	+	−	−	+	+	+
Coracina caledonica	+	+	+	+	+	+
Lalage maculosa	−	−	−	+	+	−
Lalage leucopyga	−	−	−	+	−	+
Pachycephala [*pectoralis*] *caledonica* (e)	+	+	+	+	+	+
Petroica multicolor ambrynensis	−	−	−	+	−	+
Rhipidura [*fuliginosa*] *albiscapa*	+	−	−	+	+	−
Rhipidura spilodera	+	+	+	+	+	+
Neolalage banksiana (E)	+	+	+	+	+	+
Clytorhynchus pachycephaloides grisescens (e)	+	+	+	−	+	−
Myiagra caledonica	+	+	+	+	+	−
Cichlornis whitneyi, Melanesian Thicketbird	−	−	−	−	−	+
Zosterops flavifrons (E)	+	+	+	+	+	+
Zosterops lateralis	+	−	−	+	+	+
Alponis zelandica, Rufous-winged Starling (e)	−	−	−	−	−	+
Turdus poliocephalus vanikorensis	−	+	+	+	−	+
Erythrura cyaneovirens, Red-headed Parrotfinch	−	−	−	−	−	+
Total species	25	22	16	30	30	24
Total endemic species (E + e)	8	8	6	8	11	8

50/day) generally flew much closer to the ground than the Uniform Swiftlet (*C. v. vanikorensis*; ≤20/day, except for loose flocks of ~400 that passed over on several mornings at Tsarapae, all flying west). Both species were noted at all sites visited on Santo. Despite our careful observations of all swiftlets detected on Santo, we did not record the White-rumped Swiflet (*Collocalia spodiopygia*), which was unknown to our guides.

TABLE 4. Avian specimen data from Santo, Vanuato, October–November 2002 and June 2003. Specimens collected at low elevations around Wusi and Kerevalissy villages and montane study sites are included. E = endemic to Vanuatu, e = endemic to Vanuatu plus New Caledona and/or the Santa Cruz Group. See Tables 2 and 3 for English common names. Juvenile status determined by presence of bursa of Fabricius, degree of skull ossification, condition of reproductive tract, and plumage. Breeding evidence (+ or −) determined on the basis of condition of reproductive tract, active nests, or recently fledged juveniles; NI = no information.

	Body mass (g) of specimens				Breeding evidence	
Species	Adult male	Adult female	Juvenile male	Juvenile female	Oct–Nov 2002	June 2003
Gallirallus philippensis	202, 210, 233, 244, 252	188, 252	222	156, 173	+	+
Macropygia m. mackinlayi	82	81, 82, 91, 94	70, 72	—	+	−
Chalcophaps indica sandwichensis	106, 117, 130, 134	100, 112, 118, 119	—	—	+	+
Ptilinopus tannensis (E)	202, 206	204, 221	91	—	+	+
Ptilinopus greyii (e)	86, 94, 95	65, 69, 88	83	73, 79	+	+
Ducula p. pacifica	515	—	—	—	NI	−
Ducula bakeri (E)	394	—	437	—	NI	+
Trichoglossus haematodus massena	118	102	—	—	NI	−
Tyto alba	—	301	—	—	−	NI
Collocalia esculenta uropygialis	4.8, 5.4, 5.4	4.9, 5.2, 5.9, 6.0	—	—	+	+
Todiramphus farquhari (E)	37, 39, 40.5	38, 39, 39.3	40	—	+	−
Todiramphus chloris santoensis	56.5	—	65	—	−	NI
Glycifohia n. notabilis (E)	29.7	23.3, 26.4	—	26.4	+	−
Myzomela cardinalis tenuis	11.1, 11.9, 12.0, 12.1, 13.5	8.4, 9.7, 10.0	—	—	+	+
Coracina caledonica thilenii	159	—	155	—	−	NI
Lalage maculosa modesta	24.8	25.8	—	—	+	NI
Pachycephala [*pectoralis*] *caledonica intacta* (e)	23.3, 23.8, 26.0, 26.0, 26.2	23.2, 23.9	21.4, 23.3	23.0	+	+
Petroica multicolor ambrynensis	8.4, 9.7	8.5	—	—	+	NI
Rhipidura [*fuliginosa*] *albiscapa brenchleyi*	8.1, 8.2, 8.4	7.1	7.8	—	+	+
Rhipidura s. spilodera	13.4, 13.4, 14.0	10.6, 11.0	—	11.4	+	−
Neolalage banksiana (E)	16.2, 17.9, 17.9, 18.0, 19.3, 20.2	15.5	18.1, 18.2	17.6	+	+
Clytorhynchus pachycephaloides grisescens (e)	25.0, 27.3, 28.0, 30.1	29.0	—	—	+	+
Myiagra caledonica marinae	12.8, 13.3, 14.6, 14.9, 15.7	12.1, 13.2	—	—	+	−
Zosterops flavifrons brevicauda (E)	10.2, 10.5, 10.9	10.0, 11.9	10.2, 10.3	9.9, 10.7, 11.0	+	+
Zosterops lateralis tropicus	13.3, 14.3	12.5, 13.2, 15.4	15.0	14.8	+	−
Turdus poliocephalus vanikorensis	42.5, 44.0, 46.0	46.0, 54	—	—	+	NI

Todiramphus farquhari.—Endemic to Santo, Malo, and Malakula, the Chestnut-bellied Kingfisher was slightly more common in the wet forests near Tsaraepae (≤5/day) than in the dry forests of the western slope, although we recorded up to six daily at Wunarohaehare. It was most common in high-canopy forests, but also persisted in forest patches, even near Kerevalissy village. It ranged from the lowlands up to at least 800 m, overlapping the entire elevational range of its larger congener, the Collared Kingfisher (*T. chloris*), which prefers more open habitat. The Chestnut-bellied Kingfisher was very vocal at both sites, often singing throughout the day. The call is a series of ascending notes with decreasing intervals, not the "monotonous single note" described by Bowen (1997). The two birds collected at Wunarohaehare, both at 600 m, were adult males, one in non-reproductive condition (testes 3 × 1.5 mm) and the other with somewhat enlarged testes (6 × 4 mm). Evidence of reproductive activity at Tsaraepae included a juvenile male (probably in first prebasic molt, with heavy wing molt and moderate body molt), and two adult females with convoluted oviducts but unenlarged ova. Stomachs contained the remains of large beetles (including Cerambycidae), large orthopterans, spiders, skinks, and geckos.

Glycifohia notabilis.—The monotypic White-bellied Honeyeater is endemic to Santo and Malakula. With Dickinson's (2003) placement of this species in the genus *Glycifohia* (previously classified as *Phylidonyris*), its only congener—the Barred Honeyeater (*G. undulata*)—is endemic to New Caledonia. Previously, both had been placed in the widespread Australian genus, *Phylidonyris.* The White-bellied Honeyeater occurred in similar abundance between 600 and 800 m at both sites, usually in large tracts of forest. Often, these birds congregated at flowering trees in noisy groups of ≤15 individuals. Of four specimens (two from each site), only one was reproductively active, a male from Wunarohaehare with enlarged testes. The other bird from this site, an adult female (no bursa; skull 100% ossified), had minute ova, a straight oviduct (probably had not yet bred), and its wings, tail, and body were molting. An adult female from Tsaraepae had these same characteristics. A young male (bursa 2 × 2 mm) from Tsaraepae also was molting, probably its first pre-basic molt.

Petroica multicolor ambrynensis.—The subspecies of Pacific Robin from Santo, *P. m. ambrynensis*, is one of 5 subspecies from Vanuatu and 14 across Oceania. In the Solomons and New Guinea, the Pacific Robin is restricted to montane forests. Although apparently restricted to high-elevation forests (>500 m) on Santo, the Pacific Robin may be found at lower elevations elsewhere in Vanuatu. JJK found it to be common in lowland forests on the rain-shadowed Dillon's Bay area of western Erromango. On Efate, however, DWS found it in humid, mid-elevation forest (~350 m). In addition to not finding the Pacific Robin at Tsaraepae (although our guides there knew of this species), no one has recorded it from any lowland location on the wet (eastern) side of Santo. Medway and Marshall (1975) recorded it at an elevation of 1,100 m on the eastern flank of Mt. Tabwemasana, but we recorded robins (up to four daily) only in forest from 650 to 800 m near Wunarohaehare. The three specimens were two adult males with enlarged testes and seminal vesicles, and an adult female that probably had nested recently (ova not enlarged, but oviduct somewhat thickened and convoluted).

Neolalage banksiana.—The Buff-bellied Monarch belongs to a monotypic genus endemic to Vanuatu. It occurs on most major islands south to Efate and was common at both of our primary study sites, with daily records of up to 25 at Wunarohaehare and 12 at Tsaraepae. It was found most often in pairs or family groups in the undergrowth of forest patches or large tracts of forest, especially where vine tangles or thickets of *Hibiscus tiliaceus* dominate the understory, although some birds were found in forests with an open understory.

The song of the Buff-bellied Monarch is apparently undescribed; Bregulla (1992) stated that, ". . . it is said to have melodious song." AWK tape-recorded a bird singing in scrubby dry forest adjacent to Wusi village on the morning of 25 October. The song had a stuttering, jumbled beginning, then three rapid series of reedy, high-pitched, whistled notes. The first and last series consisted of three descending notes, whereas the second series consisted of only two descending notes: *tee-*

dee-dee—tee-dee—tee-dee-deee. The song, which lasts ~3 sec, resembled that of the Fan-tailed Gerygone (*Gerygone flavolateralis*) but was shorter, and the tone of the notes was more pure. The call note (a drawn-out, single burry note that increased in amplitude) was given between songs. The song was heard (infrequently) in montane forests at Wunarohaehare as well, but not at Tsaraepae the following June. Nevertheless, Buff-bellied Monarchs called frequently throughout the day at both sites, especially pairs that called to one another while foraging.

Breeding activity of this species was pronounced at Wunarohaehare, where a near-finished nest was discovered on 1 November, 2.5 m above ground in the fork of a sapling in humid forest. The nest was similar to those described for the species by Bregulla (1992) and Bowen (1997). At least two pairs of Buff-bellied Monarchs were found accompanied by recently fledged young at Wunarohaehare. Two of the three adult males taken at Wunarohaehare had enlarged testes; the other male had somewhat enlarged testes, whereas the female lacked a bursa but had a straight oviduct, indicating that she had not bred previously. At Tsaraepae, one of the two adult male specimens had enlarged testes. The other three specimens from Tsaraepae were young birds with bursae and incompletely ossified skulls. The plumage of adult males is slightly more vividly colored than that of adult females or non-adults.

Clytorhynchus pachycephaloides grisescens.—The inconspicuous Southern Shrikebill species is found only in New Caledonia and Vanuatu. The subspecies *C. p. grisescens* is endemic to Vanuatu. Once we learned its vocalizations (see below), we recorded ≤4/day in dense forest at Tsaraepae (600–650 m). Although we netted four (in 165 net-hr) in dry forest near sea level at Wusi village, we neither netted (in 337 net-hr) nor recorded any in the higher-elevation forests at Wunarohaehare. One also was seen by AWK at the Vatte Conservation Area in northern Santo in November 2002, and the species was heard often and seen occasionally in lowland forests at the Loru Protected Area (Bowen 1997). Shrikebills were netted rarely (0.006/net-hr) at two lowland forest sites east of the main cordillera by Medway and Marshall (1975), although none was found at their higher-elevation site (1,120 m). The birds we observed were sluggish, perching from near the ground to 8 m above ground in the humid forest.

Bregulla (1992) described the Southern Shrikebill's song as highly variable "drawn out whistled sounds in cadence." On 10 June at Tsaraepae, AWK tape-recorded a three-part song made up of two evenly spaced, harsh *chek* notes, followed by a descending, drawn-out, burry whistle. The most commonly recorded call was a single, burry musical note, similar to that of the Buff-bellied Monarch, but less raspy and dropping in pitch at the end.

Testes of the male collected at Tsaraepae were somewhat enlarged (10 × 5 mm), indicating recent reproductive activity. The four taken near sea level at Wusi were adults (no bursae, skull 100% ossified) consisting of two reproductively active males (testes enlarged) and a nonbreeding male and female.

Zosterops flavifrons.—Endemic to Vanuatu, the Yellow-fronted White-eye was one of the most common forest birds at both sites, as it is throughout much of the archipelago (AWK, JJK, DWS pers. obs.). Up to 75 were found daily from near sea level to the highest elevations that we visited (1,250 m at Wunarohaehare, 700 m at Tsaraepae). We often found White-eyes in fruiting trees, where flocks of ≤15 kept up a persistent chatter. It co-occurred at some forest edges with a larger congener (*Z. lateralis*, the Silver-eye), although the latter usually was absent from the large tracts of mature forest where the Yellow-fronted White-eye was most common. At Wunarohaehare, all adult specimens were in reproductive condition (three males, two females). At Tsaraepae, all five specimens were young birds (with bursae and/or incompletely ossified skulls): two were undergoing wing molt, three were in tail molt, and all were undergoing body molt.

Turdus poliocephalus vanikorensis.—The extremely polytypic Island Thrush (51 recognized subspecies; Dickinson 2003) occurs irregularly from the Philippines to Samoa. Among the eight subspecies occurring in Vanuatu is *T. p. vanikorensis*, found on Santo, Malo, and the Santa Cruz Group. Similar to the Pacific Robin, today the Island Thrush is restricted to montane forests on some islands (e.g., New Guinea, New Ireland), whereas on others (e.g., Rennell in the Solomon Islands) it lives in the lowlands. Fossils from coastal sites in Tonga (where it no longer occurs) and New Ireland indicate that the Island Thrush has undergone considerable range contraction since the arrival of humans on the islands (Steadman 1993, 2006b).

The Island Thrush was absent at Tsaraepae but common at Wunarohaehare, where we found it in dry forests near sea level (0.03/net-hr), in montane forests at 600–800 m in elevation (0.03/net-hr), and in forest patches at 1,250 m (0.08/net hr). Birds collected near Wusi included adults of both sexes with enlarged gonads. The current distribution of the Island Thrush on Santo resembles that of the Pacific Robin in being present in dry forest on the western slopes of the cordillera but absent (or very rare) in humid forests to the east. Likewise, Bowen (1997) did not record it at the Loru Protected Area. This may reflect a recent change in its status east of the cordillera, where the Island Thrush was recorded frequently at two lowland forest sites in 1971 (Hog Harbour, Apuna River; Medway and Marshall 1975). Predation by feral cats may be the cause of the apparent decline of the Island Thrush on Santo.

DISCUSSION

Inter-site (intra-island) comparisons.—Of the 39 species of landbirds recorded from at least one of the six surveyed sites on Santo (Fig. 1, Table 3), only 17 (44%) were found at five or six sites. These included 5 of the 11 endemic or near-endemic species. Three species known from Santo (*Gallicolumba sanctaecrucis*, *Cacomantis pyrrhophanus*, *Aplonis santovestris*) were not recorded at any of the sites. That more species are not more widespread on Santo may be due to elevational factors; nine species are known only from one or more of the three highland (>500 m) sites (*Aplonis santovestris* also is restricted to highlands), and two species (*Gallirallus philippensis*, *Tyto alba*) are recorded only from lowland sites (<500 m). Of the remaining species found at fewer than five sites, some preferred more open habitats (*Todiramphus chloris*, *Rhipidura albiscapa*, *Artamus leucorhynchus*, *Zosterops lateralis*) and some were rare (*Megapodius layardi*, *Falco peregrinus*, *Gallicolumba sanctaecrucis*, *Charmosyna palmarum*, *Aplonis zelandica*); for unknown reasons, others (*Columba vitiensis*, *Ptilinopus tannensis*, *Cacomantis pyrrhophanus*, *Collocalia vanikorensis*, *Turdus poliocephalus*) occur only locally.

The inter-site variation in landbird communities on Santo is noteworthy. In island biogeography, it has been common practice to assemble lists based on the entire fauna or flora of an island, even though many species may rarely, if ever, interact because they are not syntopic. Because much of island biogeography theory (e.g., MacArthur and Wilson 1967; Diamond and Marshall 1977; Diamond 1980, 1982; Mayr and Diamond 2001) is based on analyses at the community level, it may be more biologically informative to compare the avifauna from single sites, rather than the entire avifuana of islands, especially on large islands where strong elevational and precipitation gradients occur (e.g., Santo). Aside from the massive island of New Guinea, there is no island in Melanesia for which bird survey data have been published for as many sites as those on Santo. We urge biologists working on islands to undertake the surveys needed to generate data on presence/absence, relative abundance, and habitat preference of birds from single sites.

Inter-archipelago comparisons.—Compared with a forested lowland site on the similarly sized island of Isabel (3,995 km^2; Fig. 1) in the Solomon Islands (Kratter et al. 2001a, 2001b), the species richness at the sites on Santo was much lower (25–30 versus 59 resident species of forest birds). Pigeons and doves contributed equally to richness (seven species at sites on either island), whereas passerine diversity was not as rich on Santo but contributed a higher percentage to species richness (15–16 species or 50–53% at the Santo sites, versus 21 species or 36% at Isabel). The sites on Santo also had markedly fewer hawks and falcons (one compared with five species on Isabel), parrots (two versus six species), and kingfishers (two versus six species). In addition, the sites on Santo held a smaller portion of the entire forest bird avifauna than that found along the Garanga River on Isabel: the 30 species found at either Wunarohaehare or Tsaraepae represent 71% of the 42 species known from Santo, whereas the 59 species found along the Garanga River represent 84% of the 70 species of landbirds known from Isabel. This may have been due, in part, to our longer stay at the Garanga River site (21 days over 2 years versus 6 and 7 days at Wunarohaehare and Tsaraepae, respectively). Another possible factor is that, for a given island in Oceania, lowland forests tend to support richer bird communities than montane forests (Mayr and Diamond 2001).

Species not recorded at our sites.—At Wunarohaehare and Tsaraepae, we failed to record seven species known to occur in forests on Santo—the Peregrine Falcon (*Falco peregrinus*), Santa Cruz Ground Dove (*Gallicolumba sanctaecrucis*), Fan-tailed Cuckoo (*Cacomantis pyrrhophanus*), Rufous-winged Starling (*Aplonis zelandicus*), Mountain Starling (*A. santovestris*), Melanesian Thicketbird (*Cichlornis whitneyi*), and Red-headed Parrotfinch (*Erythrura cyaneovirens*). Our guides knew the Peregrine Falcon and called it "vusavusa" in the Hakei language; it may be a rare resident at or near our sites, most likely in areas with cliffs. The Santa Cruz Ground Dove is considered rare in montane forests (Bregulla 1992); our guides, however, knew it and called it "nono." Perhaps restricted to the lowlands, the Fan-tailed Cuckoo has become rare in Vanuatu (Bregulla 1992), and our guides did not recognize it. The Fan-tailed Cuckoo also was not recorded at the other four sites surveyed in 1971 and 1995 (Medway and Marshall 1975, Bowen 1997), although Bregulla (1992) considered it uncommon on Santo.

The Mountain Starling is known to occur only in cloud forest at elevations >1,150 m on Santo (Medway and Marshall 1975), and, on the southern slopes of Peak Santo, the starling was not found below 1,400 m (Bregulla 1992). The Rufous-winged Starling is thought to be common in forests at around 1,000 m on Santo (Bregulla 1992). Although it could be absent from the drier forests on the western slope, we suspect that we would have found it on the wetter southern slopes had the rainfall diminished, thereby allowing us access to higher elevations. Our guides did not recognize the illustrations (in Bregulla 1992) of either starling species. The Melanesian Thicketbird is a streamside specialist, and we did not sample streamsides at either site. Our guides knew the species, however, explaining that it lives close to the ground along high-elevation streams; they called the male "sisivia" and the female "sisiriva." The Red-headed Parrotfinch (*Erythrura cyaneovirens*) is an uncommon fig specialist suspected of being nomadic, which likely explains its absence from seemingly suitable habitats if the large, fleshy fig fruits that it prefers (Bregulla 1992; DWS pers. obs. on Efate Island, 3 August 1997) are scarce or absent. Our guides had no name for Red-headed Parrotfinch.

Finally, bones from archaeological sites elsewhere in Vanuatu give clues about which species once may have lived on Santo. DWS and JJK have identified extinct or extirpated species of megapode (*Megapodius* undescribed sp.) and hawk (*Accipiter* cf. *fasciatus*) on Efate, flightless rail (*Porzana* undescribed sp.) and parrot (*Eclectus infectus*; Steadman 2006a) on Malakula, and starling (*Aplonis* undescribed sp.) on Erromango. Given that most volant species of Pacific Island landbirds were more widespread before the arrival of humans on the islands (Steadman 1995, 2006b), we suspect that these (or similar species in the case of flightless rails) once lived on Santo and many other islands in Vanuatu.

ACKNOWLEDGMENTS

We kindly thank D. Kalfatak and E. Bani of the Vanuatu Environment Unit for permission to undertake this research, and for logistical assistance. We are very grateful to R. Regenvanu and the staff of the Vanuatu National Museum for crucial logistical support and advice. For assistance at our field sites we thank K. Alvea, Chief Bua and the residents of Wusi, W. Dauron, M. K. Hart, R. Kolomule, Chief P. Leon and the residents of Kerevalissy, S. Nisak, R. Palo, and P. Tavouiruja. Funding (to DWS) was provided by the University of Florida Division of Sponsored Research (Research Opportunity Fund grant U001) and National Science Foundation grant EAR-9714819. We thank G. Dutson and two anonymous reviewers for constructive comments on the manuscript.

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The Wilson Journal of Ornithology 118(3):309–315, 2006

A DESCRIPTION OF THE FIRST MICRONESIAN HONEYEATER (*MYZOMELA RUBRATRA SAFFORDI*) NESTS FOUND ON SAIPAN, MARIANA ISLANDS

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ABSTRACT.—We provide the first descriptions of Micronesian Honeyeater (*Myzomela rubratra saffordi*) nests ($n = 7$) and nestlings ($n = 6$) from Saipan in the Mariana Islands. Measured nests ($n = 3$) averaged 46.7 mm in inner cup diameter, 65.7 mm in outer diameter, 41.3 mm in cup height, and 55.3 mm in external nest height. We found all nests in two species of native trees, 1.47–5.1 m above the ground. Nesting materials were primarily vine tendrils and *Casuarina equisetifolia* needles. We also report observations of parental behavior. Nests, nest placements, and behaviors appeared broadly similar to those reported for this species prior to its extirpation on Guam, and on other islands in Micronesia. *Received 2 May 2005, accepted 26 January 2006.*

The Meliphagidae family (honeyeaters) is restricted to the Australo-Papuan region (Mayr 1945). Micronesian Honeyeaters (*Myzomela rubratra*) occur throughout the high islands (i.e., those of volcanic origin rising more than a few meters above sea level) of Micronesia, with subspecies endemic to Palau (*M. r. kobayashii*), Yap (*M. r. kurodai*), Chuuk (*M. r. major*), Pohnpei (*M. r. dichromata*), Kosrae (*M. r. rubratra*), and the Mariana Islands (*M. r. saffordi*; Pratt et al. 1987). Within the Mariana Islands, Baker (1951) found that birds from Guam, Rota, Tinian, and Saipan are similar with respect to morphometric measurements, and he does not separate them taxonomically. Micronesian Honeyeaters, along with most other native forest birds, were extirpated from Guam in the mid-1980s with the arrival and range expansion of the brown treesnake (*Boiga irregularis*; Savidge 1987, Wiles et al. 2003). Surveys on Rota, Tinian, and Saipan (the inhabited islands of the Commonwealth of the Northern Mariana Islands [CNMI]) have indicated that Micronesian Honeyeaters are less numerous on Saipan than on Rota or Tinian (Pratt et al. 1979, Ralph and Sakai 1979, Jenkins and Aguon 1981, Jenkins 1983, Craig 1996), although Engbring et al. (1986) found that densities were greater on Saipan than on Tinian. On Saipan, Engbring et al. (1986) counted 549 honeyeaters (mean of 2.25 birds per station ± 0.14 SE), and estimated the total Micronesian Honeyeater population at 22,573. In a repeat survey, the U.S. Fish and Wildlife Service (1997) counted 316 honeyeaters (mean of 1.30 birds per station ± 0.09 SE; no population estimate given), indicating a possible decline in the honeyeater population between survey periods.

Little research has been published on the avifauna of the Mariana Islands, and many detailed aspects of life histories are unknown for most native and endemic species (Rodda et al. 1998, Mosher and Fancy 2002). This lack of information hampers the development and implementation of conservation plans. Despite interdiction measures, the number of brown treesnake sightings on Saipan has increased in recent years (Rodda et al. 1998; N. B. Hawley pers. comm.); although definitive proof is lacking, 75 plausible brown treesnake sightings and 11 hand-captured brown treesnakes on Saipan (Gragg 2004) indicate that an incipient population of snakes is now established (Colvin et al. 2005). Thus, information on the ecology and breeding biology of all avian species in the CNMI is urgently needed so that captive breeding programs can be implemented.

We undertook a study to assess nesting success of common forest passerines in native and nonnative forests of Saipan. Micronesian Honeyeaters were not a target species for this study, as they are reported to be more com-

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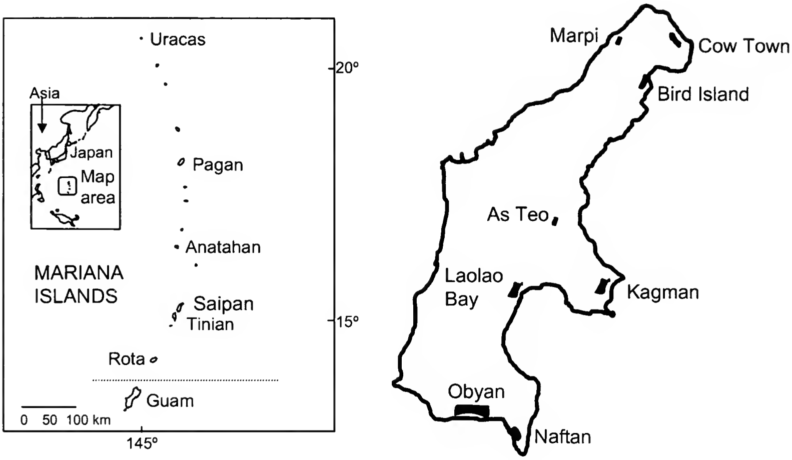

FIG. 1. Location of Saipan within the Commonwealth of the Northern Mariana Islands, and Saipan study sites (shaded areas) in which we searched for nests of native forest birds during 2003 and 2004 to assess nesting success; Micronesian Honeyeater nests were found at Marpi, As Teo, Kagman, and Laolao Bay. Marpi, As Teo, and Kagman study areas were native forest; Cow Town, Bird Island, Obyan, and Naftan were nonnative tangantangan forest; Laolao Bay was mixed native/agriforest. Approximate coordinates (taken at the nearest open area, generally a road) for study sites were as follows: As Teo 15° 11′ N, 145° 45′ E; Bird Island 15° 15′ N, 145° 48′ E; Cow Town 15° 16′ N, 145° 49′ E; Kagman 15° 09′ N, 145° 16′ E; Laolao Bay 15° 09′ N, 145° 44′ E; Marpi 15° 16′ N, 145° 47′ E; Naftan 15° 06′ N, 145° 44′ E; Obyan 15° 06′ N, 145° 43′ E. The dotted line on the location map signifies the division between the Territory of Guam and the Commonwealth of the Northern Mariana Islands.

mon in coconut plantings, shrubbery and gardens of villages, scrub, coastal strand, and diverse second-growth forest composed of both native and introduced trees (Seale 1901, Safford 1902, Pratt et al. 1979, Jenkins 1983, Engbring et al. 1986). Over the course of our study, however, we incidentally found seven Micronesian Honeyeater nests. To our knowledge, these are the first nests of this species found on Saipan, although nests have previously been found on Guam, and one nest has been found on Rota. Here, we describe nests and nestlings from Saipan and compare these descriptions with those from Guam, Rota, and other islands in Micronesia from which information is available.

METHODS

Study area.—Saipan, located in the western Pacific Ocean (15° 10′ N, 145° 45′ E; Fig. 1), encompasses a land area of 123 km^2, and is the second largest island in the Marianas. The island has a tropical climate with an annual mean temperature of 28.3° C and mean annual rainfall of 200–250 cm. The timing of the wet and dry seasons varies somewhat between years, but the wet season usually extends from July to November and the dry season from December to June. Typhoons may occur at any time, but are most frequent between August and December (Young 1989, Mueller-Dombois and Fosberg 1998).

We focused our study on two forest types—introduced tangantangan (*Leucaena leucocephala*) forest and native limestone forest. Most (77%) of the forest remaining on Saipan is nonnative (Falanruw et al. 1989), and tangantangan forest is estimated to cover 28% of the island. This tree species grows in dense, near-monocultures on flat lowlands and plateaus (Craig 1990). Native limestone forest is restricted to cliffs and less accessible areas not easily cultivated (Craig 1989, Stinson and Stinson 1994), and is estimated to cover only 5–19% of Saipan (Engbring et al. 1986, Young 1989). *Pisonia grandis* and *Cynometra ramiflora* dominate the canopy of this forest type, and *C. ramiflora* and *Guamia mariannae* are the most common species in the understory (Craig 1996). Study sites were selected in three native, four nonnative, and one mixed forest (Fig. 1). The mixed forest contained common native and agriforest trees, including coconut (*Cocos nucifera*) and mango (*Man-*

gifera indica). Study areas were delineated by transects marked with flagging.

Avian surveys.—We conducted our study from April to July 2003 and February to May 2004. Micronesian Honeyeater nests were found while searching line transects according to distance sampling methodology (Buckland et al. 2001) or incidentally while moving through the forest to monitor nests of other species. When found, each nest was flagged and assigned a unique nest identification number. Nest contents were visually checked and described at 3-day intervals, using a mirror on a telescoping pole if necessary. We did not handle nest contents while nests were still active; thus, no egg measurements were made, and we visually estimated nestling characteristics by using a millimeter ruler for comparison.

After each nesting attempt was completed, we measured the nest's height, distance from trunk, and number and diameter of supporting branch(es). Tree species and tree height were also recorded. We used a clinometer to measure nest and tree heights (unless these could be measured directly with a steel measuring tape), a steel measuring tape to measure distance from the trunk, and a millimeter ruler to measure diameters of supporting branches. We also estimated the distance between the nest and the nearest road in 25-m categories (≤25, 26–50, 51–75, 76–100, and >100 m). Nests were collected if possible and measured with a millimeter ruler, after which they were labeled and given to the CNMI Division of Fish and Wildlife on Saipan.

RESULTS

We discovered seven honeyeater nests on 31 May 2003, and on 17 February, 9 March, 12 March, 7 April, 9 April, and 26 April 2004. Two nests contained eggs, two contained nestlings, and two were empty when located. The female was sitting on one nest and was not disturbed; in this case the nest contents were not determined when the nest was discovered. No adults were in attendance at three nests upon initial discovery. Four nests failed (three during incubation and one at an undetermined nesting stage), and three fledged young. Four nests were located in mixed forest, and one nest was located in each of the three native sites. All six nests in which we observed contents contained two eggs or two young. Initially, we mistook two nests for Bridled White-eye (*Zosterops conspicillatus saypani*) nests due to their similar size, structure, and placement. However, we noticed that the nests of Micronesian Honeyeaters tended to have thinner walls and deteriorated more rapidly than Bridled White-eye and Golden White-eye (*Cleptornis marchei*) nests, which they otherwise closely resembled.

Nest composition and structure.—Only three nests were accessible and in adequate condition for measurement. Cup heights were 39, 40, and 45 mm (mean = 41.3 mm), and nest heights were 41, 50, and 75 mm (mean = 55.3 mm). Internal diameters were 43, 47, and 50 mm (mean = 46.7 mm), and external diameters were 55, 69, and 73 mm (mean = 65.7 mm). Nests were composed of vine tendrils and *Casuarina equisetifolia* needles (Fig. 2), and part of a leaf skeleton from a native *Pandanus* sp. was entwined around the outer base of one nest.

Nest placement.—Micronesian Honeyeater nests were located at various distances from roads (i.e., from <25 to >100 m). Four nests were placed in *Guamia mariannae* and three were placed in a *Psychotria* (genera comprising more than one species in CNMI, and which we could not identify to species level, are listed herein only to the genus level). Nest (and tree) heights in *G. mariannae* were 1.5 m (5.6 m), 3 m (5 m), 3.5 m (6 m), and 5.1 m (not obtained), and in *Psychotria* they were 1.5 m (2 m), 1.7 m (2.3 m), and 3.8 m (8 m). Nests were placed 83–184 cm from the trunk in *G. mariannae* and 0–103 cm from the trunk in *Psychotria*, generally near the outer edge of the tree (Fig. 2). The number of nest support branches varied from two to five in both tree species, and support branch diameter ranged from 1.5 to 9.7 mm in *G. mariannae* and from 1.5 to 2.5 mm in *Psychotria*.

Egg description.—Although four monitored nests each contained two eggs, we had a clear view of the eggs only in the nest found on 26 April 2004. The eggs were creamy white and marked with two distinct rings of brown speckles, one ring near the broad end and the other near the narrow end of the egg.

Nestling description.—Of the three nests from which young fledged successfully, we found two during the nestling stage and one

FIG. 2. Micronesian Honeyeater (*Myzomela rubratra saffordi*) nest photographed on Saipan, Mariana Islands, 19 April 2004, showing its placement at the outer end of the branch.

during the incubation stage. Micronesian Honeyeater nestlings are altricial and closely resemble Bridled White-eye nestlings until they develop red pin feathers. Because nestling development was variable, each nest is treated separately.

The 2003 nest contained eggs when found, and the two nestlings were first seen at day 0–1 following hatching. At this age they were estimated to be approximately 2 cm in length, had dark pink skin, and were downy on their wings and backs. On day 3–4, the nestlings had grown to 3–3.5 cm in length, were still covered with down, and their skin color was dark pink/purple. They appeared well fed, as they had large, rounded stomachs. At day 6–7, when their eyes were beginning to open, the nestlings were 4–4.5 cm long, with wing pins approximately 5 mm in length and back pins beginning to erupt. Their heads were covered in long down. On day 7–8, the chicks were still 4–4.5 cm long, their wing and back pins were 8 and 2 mm (respectively) long, their bills were beginning to curve, and their head pins still had not erupted. Underlying skin color, which lightened progressively throughout nestling development, was pale pink by this stage. At day 9–10, the wing pins were 10 mm in length and tail and head pins had erupted 1 mm. Tan brown feathers had erupted from the wing pins, red feathers were beginning to erupt from the back pins, and 1- to 2-mm head pins were visible on day 10–11. Both nestlings fledged prematurely on day 13–14, when the observer was 1 m from the nest. One nestling was captured and returned to the nest, but the second could not be relocated and was left to the adults who remained nearby and were agitated. At this time, the nestlings were estimated at 5.5 cm in length, but they were not yet fully feathered. Red feathers, 1 mm in length, had erupted on the back, gray feathers had erupted on the head, and 8-mm tail pins did not yet have erupted feathers. The breast was bare. On day 14–15, the remaining nestling's wing feathers had turned dark gray, and it fledged at day 15–16.

The second nest that fledged young was found on 12 March 2004. On that date, the two nestlings were already approximately 4 cm in length, their eyes were open, and they had 2-mm long downy feathers erupting from the pins on their wings, backs, and heads. On 15 March, only one nestling remained. This nestling fledged prematurely on 18 March when the observer approached to ~3 m from the nest. The nestling fluttered away, but it could not fly and was captured and returned to the nest. We estimated the nestling to be 4–4.5 cm long and it did not appear fully feathered. The erupted feathers were mostly black, with small red patches of feathers appearing on the head and back. By 22 March, when the final nest check was performed, this nestling had fledged.

On 9 April 2004, we found the last successful nest by observing the female bringing food to her two nestlings. The nestlings were estimated at 3–3.5 cm in length and were already developing pin feathers. On 13 April, the nestlings were ~4 cm long, covered with long, black pins from which feathers had erupted, and their eyes were open. Three days later, the nestlings were 4–4.5 cm long and their bills were visible over the rim of the nest. They were black all over with no red feathers visible. By 19 April, the nestlings had fledged.

Parental behavior.—Only females were observed incubating (n = 5 nest checks) or brooding nestlings (n = 1 nest check). However, one or both members of the pair were often observed close to the nest. When observed, the adult(s) were always very agitated. Typically, one or both adults would feign injury, fluttering about low to the ground and drooping one wing. If only one adult was present, this behavior was sometimes accompanied by scolding; if both adults were present, one adult would often feign injury while the other scolded. We observed injury-feigning behavior on 9 of 26 nest visits and scolding during 5 of 26; this behavior was observed only at nests containing nestlings. Micronesian Honeyeaters appeared very intolerant of disturbance at the nest during the incubation stage, as each time the incubating female was flushed from the nest during a nest check (n = 3), the nest had failed by the next visit.

DISCUSSION

Prior to our study, nests of Micronesian Honeyeaters had been found on Guam (Hartert 1898, Seale 1901, Yamashina 1932, Jenkins 1983; N. Drahos pers. comm.), Rota (C. C. Kessler unpubl. data), Kosrae and Pohnpei (Baker 1951), Chuuk (Baker 1951, Brandt 1962), Palau (Pratt et al. 1980), and in the southwest Pacific region (Mayr 1945). The amount of information provided varies by source. Nest measurements are variable, with the following ranges reported from Guam: cup height 25–50 mm, outer height 50–120 mm, internal diameter 25–60 mm, and external diameter 35–80 mm (Hartert 1898, Seale 1901, Jenkins 1983; N. Drahos pers. comm.). The measurements of nests we found on Saipan fall within these ranges. In contrast, the average outer height of 18 nests found on Chuuk was 20 mm, considerably shorter than nests from Guam and Saipan, although the average external diameter was similar (50 mm; Brandt 1962). Our nest heights are also similar to those reported from other islands, varying from 1.2 to 4.6 m (Hartert 1898, Seale 1901, Yamashina 1932, Mayr 1945, Brandt 1962, Jenkins 1983; N. Drahos pers. comm., C. C. Kessler unpubl. data).

Similar to our descriptions of nests found on Saipan, nests from Guam, Rota, Chuuk, and Palau have been variously described as "loosely constructed," "fragile," "frail," "not heavily made," and having see-through sides (Brandt 1962, Pratt et al. 1980, Jenkins 1983; C. C. Kessler unpubl. data). In addition, they were found placed among the outer branches of the trees in which they were constructed (Seale 1901, Brandt 1962, Pratt et al. 1980, Jenkins 1983). Unlike the nests we found on Saipan, however, those on other islands tended to be found in open locations, such as the edges of clearings or the outer perimeters of forests (Brandt 1962, Pratt et al. 1980; C. C. Kessler unpubl. data). Reported nesting materials are diverse and include fine roots and fibers, grasses, leaves, ferns, weed stems, and pieces of coconut bast (Mayr 1945, Baker 1951, Brandt 1962). As on Saipan, *Casuarina equisetifolia* needles were included in nests found on Guam.

The chief difference between our observations and those of other authors in the Mariana Islands is the suite of tree species used for nesting. On Saipan, nests were placed in *Psychotria* and *Guamia mariannae* (trees native to the Mariana Islands), whereas nests on Guam were placed in *Pithecellobium dulce*, *Casuarina equisetifolia*, *Delonix regia*, and *Bruguiera gymnorrhiza*, only two of which (*C. equisetifolia* and *B. gymnorrhiza*) are indigenous to the Mariana Islands (Raulerson and Rinehart 1991). On Rota, the nest was found in nonnative *Acacia confusa*. This difference is likely a reflection of other authors working primarily in habitats that were different from those in which we worked (only one of our study areas comprised mixed native and exotic forest), rather than differences in honeyeater habitat use among islands.

All reported clutch sizes are of one or two eggs, although a nest found on Palau contained three nestlings (Pratt et al. 1980). Two- to three-egg clutches are characteristic of the Meliphagidae family (Mayr 1945). Micronesian Honeyeater eggs from Saipan, Guam, Rota, and Chuuk all had a base color of white, off-white, or cream, generally with rufous-brown speckling, although Yamashina (1932) described the speckling as gray and dark yellow-brown. The speckling may be concentrated at the broader end (Hartert 1898, Seale 1901, Brandt 1962, Jenkins 1983), near the narrow end (Yamashina 1932), near both ends (this study), or may be scattered over the whole egg (Brandt 1962).

We found no comparative descriptions of nestlings or data on their age at fledging. However, several authors have described fledgling Micronesian Honeyeaters from Guam. Seale (1901:57) reported that ". . . the young are olive brown above, yellowish on the under parts, washed with red on the sides of the fore breast and back; bill dark, yellowish on the base of lower mandible; feet and iris dark." N. Drahos (pers. comm.) described a pair of fledgling Micronesian Honeyeaters recently out of the nest. The female was mouse gray with a faintly rusty-red chin, her bill was black with a yellow stripe on its edge and the top of her bill was yellow at the base, and her eyes and feet were black. He reported that the male was similar, but the middle of the back, chin, and lower half of the head were faintly cardinal red. Other authors' descriptions are similar although less comprehensive. There are several dissimilarities among our descriptions of nestlings from different nests, and between our descriptions of nestlings and those of other authors. The former may be explained by factors that could affect nestling development, including the number of nestlings present in the nest (thus, whether provisioning must be shared), breeding experience or foraging ability of the adults, or food availability in different study areas. The latter presumably is explained by continued plumage development after fledging. Although our sample size included only two nests, Micronesian Honeyeater nestlings seem apt to leap from the nest before they are fully ready to fledge, which, under undisturbed conditions, seems to be at 15–16 days. Parental distraction displays of Micronesian Honeyeaters on Saipan appear to be the same as those of birds on Guam and Rota, although on Guam and Rota only females have been reported to feign injury (Stophlet 1946, Jenkins 1983; N. Drahos pers. comm.).

Three of the seven nests we found on Saipan were in native limestone forest, which has not previously been reported as preferred habitat for the Micronesian Honeyeater; the species has been considered more common in coconut plantings, shrubbery and gardens of villages, and diverse second-growth forest. Similarly, Cardinal Honeyeaters (*Myzomela cardinalis*) in Samoa are most abundant in village habitats (Freifeld 1999), and Orange-breasted Honeyeaters (*Myzomela jugularis*) in Fiji are most abundant in coconut plantations (Steadman and Franklin 2000). This underscores the importance of obtaining ecological information for all native species to further the development of conservation plans. Some of the habitats in which Micronesian Honeyeaters are reportedly common, such as backyard gardens, would appear unsuitable as nesting habitat, given this species' apparent intolerance of disturbance at the nest and the likelihood of disturbance in these areas.

Overall, we found that Micronesian Honeyeaters on Saipan have nesting requirements and behaviors similar to those on Guam prior to their extirpation. Information on the nesting requirements of Micronesian Honeyeaters on Saipan should aid in the establishment of effective captive breeding programs for this species, and for future re-establishment on Guam and Saipan (if necessary) once brown treesnakes have been controlled or eradicated.

ACKNOWLEDGMENTS

This study was funded by the U.S. Fish and Wildlife Service (USFWS) Region 1 Office, Portland, Oregon. We extend special thanks to the USFWS Marianas Team, in particular H. B. Freifeld and A. P. Marshall; the Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife, especially J. B. de Cruz, L. Williams, S. Kremer, and N. B. Hawley; J. Quitano for allowing us access to As Teo; N. Johnson and S. Mosher for helpful field information; and S. Hopken for translating the Yamashina (1932) paper. We appreciate the constructive comments made on earlier drafts of the manuscript by J. B. de Cruz, A. B. Franklin, R. A. Hufbauer, R. J. Craig, and two anonymous referees.

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The Wilson Journal of Ornithology 118(3):316–325, 2006

WITHIN-PAIR INTERACTIONS AND PARENTAL BEHAVIOR OF CERULEAN WARBLERS BREEDING IN EASTERN ONTARIO

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ABSTRACT.—The Cerulean Warbler (*Dendroica cerulea*) is currently the focus of considerable management interest; however, our ability to develop effective management strategies is hampered by a dearth of life history and basic behavioral data. Here, we present information on male-female interactions of Cerulean Warblers and parental nest attentiveness that is, to our knowledge, among the first such rigorously collected data for this species. Males feed females during nest building and on the nest during incubation; the relative infrequency of these events suggests that they play more of a role in pair-bond maintenance than they do in enhancing female energetics. Female incubation rhythms were not significantly influenced by temperature, time of day, or egg age. Compared with other *Dendroica* warblers, we observed relatively infrequent female departures during incubation, perhaps in response to a high risk of nest predation. As the nestlings aged, females spent less time brooding nestlings, presumably to allow for more frequent feeding; however, both males and females exhibited relatively low rates of food delivery compared with other *Dendroica* warblers. Despite the low rates of food delivery, feeding trips were more frequent at successful nests than unsuccessful nests. Our results suggest that Cerulean Warblers are tightly constrained by the competing pressures of predation risk and sufficient food provisioning for nestlings. *Received 28 February 2005, accepted 23 February 2006.*

Birds that form socially monogamous pairs during the breeding season exhibit various acoustic (Kroodsma and Miller 1996) and behavioral (Birkhead and Møller 1992) within-pair interactions. These social behaviors can have conservation and management implications; indeed, our ability to manage or conserve species of interest is often unwittingly limited by our poor understanding of basic life history and behavioral phenomena (Komdeur and Deerenberg 1997). Hopefully, the careful documentation of these behaviors will assist us in identifying species' social requirements, which may be used to augment management and conservation strategies based on habitat requirements. The Cerulean Warbler (*Dendroica cerulea*) is a poorly known species of particular concern due to population declines of up to 3% per year since 1966 (North American Breeding Bird Survey data; Robbins et al. 1992, Link and Sauer 2002), probably due to habitat loss in both North America and South America. In the United States, the species has been variously designated as threatened, rare, or of special concern; in Canada, it is a species of special concern (Robbins et al. 1992, Hamel 2000, Committee on the Status of Endangered Wildlife in Canada 2003); and it is listed as vulnerable by the International Union for Conservation of Nature and Natural Resources (2004). However, the design and implementation of effective conservation and management strategies has been slowed by limited availability of life history and behavioral data (Hamel et al. 2004).

As a result of long-term research, beginning in 1994 at the Queen's University Biological Station (QUBS) in Ontario, Canada, we have learned a great deal about habitat selection behavior (Jones et al. 2001; Jones and Robertson 2001; Barg et al. 2005, 2006), reproductive ecology and population dynamics (Oliarnyk and Robertson 1996, Jones et al. 2004), and population structure (Gibb et al. 2005, Jones et al. 2005, Veit et al. 2005) for the enigmatic Cerulean Warbler. Here, we present data on Cerulean Warbler male-female interactions and parental nest attentiveness that is, to our knowledge, among the first such rigorously collected data for this species. Specifically, we were interested in how males and females coordinate reproductive activities, how they divide parental responsibilities, and how patterns of nest attendance were influenced by weather variables, partner behavior, and nesting stage.

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METHODS

We collected data during the breeding seasons (May–July) of 1999–2001, at QUBS, Lake Opinicon, Leeds/Frontenac counties, Ontario, Canada (44° 30′ N, 76° 20′ W). The forest there is characterized as second growth deciduous, between 80 and 90 years old. The canopy is dominated by sugar maple (*Acer saccharum*), bitternut hickory (*Carya cordiformis*), and ash (*Fraxinus* spp.); the mid- and understories are primarily hophornbeam (known as ironwood in Canada; *Ostrya virginiana*) and sugar maple saplings. We used microclimate data loggers (Onset HOBO® H8 Pro Series data loggers, Bourne, Massachusetts) to record temperature and relative humidity hourly at two separate locations within the study site, which was a 24-ha area on QUBS property.

Each year, we captured territorial males by using target-netting techniques (whereby a mist net was erected in a male's territory and a conspecific playback and model presentation were placed nearby to attract the male towards the net). We banded all males with unique combinations of color bands and a Canadian Wildlife Service band. Females were more difficult to capture, as they were largely unresponsive to playbacks; thus, we attempted other methods, including chickadee mobbing calls, hoop nets placed at nests, and owl calls with presentations of owl models, to capture females. The few females we did catch (also banded) were captured opportunistically when they were visiting water sources, feeding fledglings low in the canopy, collecting nesting material, or flushed off nests low in the canopy.

The Cerulean Warbler's breeding season in Ontario is approximately 60–75 days. Over the course of our long-term study (1996–2001; 201 nests), we determined that nest building takes 4–7 days, egg laying ≤7 days, and incubation 10–12 days; the nestling stage lasts 10–11 days. The female does all the incubating and brooding, and both males and females feed the young. Nests were checked every 2–3 days. Mirrors attached to telescoping poles were used to see into the nests; if a nest could not be reached with the mirrors, we used parental activities, such as departure frequency, food delivery, or fecal sac removal, to assess nesting status.

We classified nests that fledged at least one young as successful. As the high location of nests made it difficult to determine their fates precisely, we combined all unsuccessful nests for analyses, whether they had succumbed to predation, exposure, abandonment, or some unknown cause. We hired a professional tree-climber to access nests during the nestling stages in 2000–2001. On average, it took >3 hr per nest to access and process the nestlings. Mean brood size in the nine nests that we accessed was 3.3 nestlings (range = 3–4).

To document parental behavior and within-pair interactions, we performed a series of focal nest watches in 1999–2001. For each watch, a single observer monitored activity at a nest for 30 min. Female presence or absence at the nest was recorded every minute. The observer also kept a running tally of departure/arrival times, male and female vocalizations, male visits to the nest, and feeding trips made by the male and the female—documenting the food item whenever possible. Given our inability to access most nests, we were not able to calculate provisioning rates on a "per nestling" basis, which would have allowed us to control for any potential effects of brood size on provisioning rates. Nest watches were performed on individual nests at 2- to 3-day intervals until the nestlings fledged or the nest failed; nest status was monitored between watches. Where nest visibility permitted, we videotaped nests for 2-hr periods; this allowed us to assess the bout length of incubation and brooding without the 30-min time constraint of focal-nest watches. To increase our nest-watch sample size, we included the first 30 min of each video recording in our analyses; there were no significant differences in the patterns of incubation and brooding between our focal nest watches and the first 30 min of our video recordings (all $P > 0.20$). No nest was watched or videotaped more than once on any given day.

Analysis.—We used analysis of covariance (ANCOVA) to analyze incubation patterns based on 130 watches (117 direct, 13 video) from 39 nests and 31 females conducted during 1999–2001; this included nests of females that renested ($n = 7$). Fixed effects in the ANCOVA models were time of day and day of incubation, with ambient temperature included as a covariate. Because we performed multiple watches on each female, "individual" was included in the model as a random effect. To control for seasonal effects (Julian date was significantly correlated with ambient temperature: $r = 0.45$, $P < 0.001$), we regressed time spent incubating per 30-min watch on Julian date and used the residuals from this linear regression as the response variable in the ANCOVA model.

We used ANCOVA to analyze brooding patterns based on 135 watches (111 direct, 24 video) from 40 nests and 35 females during 1999–2001. Fixed effects in the ANCOVA models were time of day and nestling age. As in the incubation models, we included "individual" as a random effect. We conducted separate analyses for two covariates: ambient temperature and male feeding rates. For the temperature model, we used the residuals from a regression of time spent brooding on Julian date as our response variable. For the male-feeding model, the response variable was the time spent brooding per 30-min watch (untransformed). In our analysis of male feeding rates, we only included 2000–2001 data (77 watches, 31 nests, 25 females). We had to exclude 1999 male feeding rate data due to consistent observer bias detected in that year; one field assistant neglected to consistently record whether or not a male was carrying food upon arrival at the nest. We also used ANCOVA models to examine the effect of ambient temperature and male feeding rate on the number of feeding trips made by females. As in the incubation and brooding models, we included "individual" as a random effect. Male feeding rate data were excluded.

We performed *t*-tests to compare time spent incubating and brooding, and the number of feeding trips (per 30-min watch) at successful versus unsuccessful nests. There was no statistically significant difference between the average timing (defined by incubation day) of watches on successful (mean incubation day of watches = 7.3 ± 0.4) and unsuccessful (mean = 7.2 ± 0.4) nests ($t = 0.14$, df = 128, $P = 0.89$). In addition to nest success (i.e., whether or not a nest fledged at least one young), we also included an analysis of survival by nesting stage (i.e., whether or not a nest survived the incubation period) because parental activity during the incubation phase is known to affect nest success (Martin and Ghalambor 1999, Ghalambor and Martin 2002). No nest watches were performed on unsuccessful nests after day 10 of the brooding period; therefore, all watches conducted after day 10 at successful nests were excluded from our analysis of parental behavior. In this restricted data set, there was no statistically significant difference between the average timing (defined by brooding day) of watches on successful (mean brooding day of watches = 5.4 ± 0.4) and unsuccessful (mean = 5.0 ± 0.1) nests ($t = 1.77$, df = 104, $P = 0.08$). Data are presented as untransformed means ± SE. All statistical analyses were performed using JMPIN (ver. 4.0.2; SAS Institute, Inc. 2000).

RESULTS AND DISCUSSION

Reciprocal vocalizations.—We documented 136 instances of reciprocal vocalizations (male vocalization followed immediately by female call) during the study period. In the context of reciprocal vocalizations, males were more likely to sing quiet songs (whisper songs) during nest building than during the other stages of the nesting cycle (nest building: 62% of reciprocal vocalizations; incubation: 18%; brooding: 24%; $\chi^2 = 23.09$, df = 2, $P < 0.001$). When females are nest building, males tend to follow very closely (often within 1–2 m) and regularly sing whisper songs directed at the female (JJB pers. obs.). Presumably, this following behavior during the fertile period is a form of mate guarding, while the whisper singing with occasional female response presumably functions in pair-bond maintenance. Our observations of male whisper singing during nest building are similar to John and Kermott's (1991) observations of the House Wren (*Troglodytes aedon*); whisper singing by male House Wrens also may serve to stimulate ovulation in the females (Johnson and Kermott 1991). Interestingly, male Cerulean Warblers would frequently whisper sing while females inspected potential nest sites; males would usually inspect these same sites immediately thereafter (JJB pers. obs.). Males were rarely heard whisper singing away from the female or the nest (Barg et al. 2005). Whisper singing by males in similar contexts has been observed in other parts of the breeding range (Rogers 2006).

Nearly two-thirds (63%) of the reciprocal observations occurred during the incubation stage, although the function of reciprocal vocalizations while the female is incubating is unclear. One possibility was that male vocalizations signal an "all-clear" for females to leave the nest; however, this was not supported by our data, despite our expectations based on anecdotal observation prior to data collection. The frequency of male whisper songs versus normal songs did not influence whether or not a female stayed on the nest following the reciprocal vocalization (Fisher's exact test, $P = 0.45$). Future research should be designed to test a second possibility, that a female response to a male vocalization may encourage male care (Halkin 1997).

Females regularly chip (without prompting by male song) when departing the nest for an off-bout (approximately 50% of departures; JJB pers. obs.), possibly as a signal to males that the nest is unprotected (e.g., Barber et al. 1998). During a survey of 15 songbird species in which females gave nest-departure calls, McDonald and Greenberg (1991) reported that, unlike the Cerulean Warbler, most of the species inhabit grassy or shrubby habitats and that the calls appear to reduce male activity at the nest, presumably to reduce the risk of predation. Male Cerulean Warblers frequently attended the nest for the duration of the female's off-bout, sitting quietly <2 m from the nest in the nest tree; sometimes the male perched on the edge of the nest but was never observed sitting on the nest (i.e., no incubating or brooding) during our watches. Apparently, males of other species are also known to exhibit nest vigilance during female absences (e.g., Northern Mockingbird, *Mimus polyglottos*; Breitwisch et al. 1989).

Mate feeding and mate quality.—We made 28 observations of males feeding females (i.e., courtship feeding) during nest building. Over half ($n = 15$) of these feeding events were followed by copulations. In all cases, the food item presented was a larval lepidopteran. Thirty-five percent of the males (16 of 46) also were observed feeding incubating females (mean = 0.70 ± 0.06 feedings/hr).

Originally, mate feeding was hypothesized to strengthen pair bonds (Lack 1940) or to serve as an index of mate quality—thereby influencing future mate choice (Nisbet 1973). More recently, researchers have shown that mate feeding can represent an important nutritive and energetic contribution to the female (Royama 1966; Lyon and Montgomerie 1985, 1987; Hatchwell et al. 1999) and may compensate for poor-quality territories (Lifjeld and Slagsvold 1986). Finally, mate feeding may serve to reduce the incidence of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), presumably by reducing female activity and keeping her on the nest; this advantage, however, may carry the cost of increased nest predation resulting from greater levels of male activity at the nest (Tewksbury et al. 2002).

The hypotheses regarding nutrition and energetics are unlikely candidates for explaining mate feeding among Cerulean Warblers, primarily because their relative frequency of mate feeding is low (less than one visit per observation hr); however, it is not clear how frequent mate feeding must be before it significantly affects female condition. Assessing the potential selection pressure of brood parasitism on mate feeding requires feeding data from nests that were parasitized; however, despite a high density of cowbirds in the region (JJ unpubl. data), we have never observed Cerulean Warbler parents feeding cowbird nestlings or fledglings. Furthermore, since 1994 we have detected cowbird eggs in only two Cerulean Warbler nests, both of which were abandoned.

We have made several observations that offer indirect support for the notion that female Cerulean Warblers are capable of assessing mate quality and potentially basing their mate-choice decisions on those assessments. First, we witnessed extra-pair copulations by banded individuals and, for the two complete families for which we obtained blood samples (on a separate project), >50% (4/7) of young were sired by a male other than the social mate (JJB unpubl. data). The criteria female Cerulean Warblers use to choose extra-pair mates are unknown, but presumably they involve judgments of male quality. Second, we observed an instance of double brooding (i.e., initiation of a second nest following a successful first nest). Double brooding may occur more frequently, but our difficulty in capturing females limits our understanding of certain reproduc-

TABLE 1. Incubation patterns (n = 130 focal nest watches) of female Cerulean Warblers at the Queen's University Biological Station, eastern Ontario, 1999–2001, were not affected by time of day, incubation day, or ambient temperature. During the nestling stage (n = 135 focal nest watches), females spent less time brooding as nestlings aged. No interactions were statistically significant (all $P > 0.10$) in these ANCOVA models. Boldface values denote significant model effects. The male feeding-rate model is based on 2000–2001 data only.

Source of variation	Mean square	df	F	P
Incubation patterns (R^2 = 0.38)				
Time of day	2.03	1	0.24	0.62
Incubation day	9.65	13	1.15	0.32
Ambient temperature (covariate)	11.59	1	1.39	0.24
Individual female	8.29	30	0.99	0.49
Error	8.36	84		
Brooding patterns				
Temperature as covariate (R^2 = 0.57)				
Time of day	12.18	1	0.30	0.58
Nestling age	160.84	13	4.02	**<0.001**
Ambient temperature	11.36	1	0.28	0.60
Individual female	51.63	34	1.29	0.18
Error	40.06	85		
Male feeding rate as covariate (R^2 = 0.58)				
Time of day	2.53	1	0.07	0.80
Nestling age	113.67	11	3.00	**0.006**
Male feeding rate	22.09	1	0.56	0.57
Individual female	35.22	24	0.93	0.57
Error	37.92	39		

tive behaviors. What makes this single observation germane is that this female was the secondary female of a bigamous male, who provided very little parental care to her first brood; once her fledglings were sufficiently mobile, the female moved the brood ~800 m (the width of four territories) and re-mated with a different male (all birds were banded). The female's choice of a second mate appeared to be based on this male's willingness to provide parental care to her fledglings, something not offered by her first mate. This second male "adopted" her brood by feeding the young while the female built a new nest and laid a clutch of five eggs (this second nesting attempt was unsuccessful). Although this is the first documented case of brood adoption in Cerulean Warblers, it has been documented occasionally in other wood warblers (e.g., Hooded Warbler, *Wilsonia citrina*; Evans Ogden and Stutchbury 1994). Interestingly, the double-brooded female's new mate already had an active nest and his primary female was incubating at the time of brood adoption. Bigamy is uncommon but regular on our study site (~10% of breeding males are bigamous; JJB pers. obs.).

Incubation patterns.—On average, females spent 25.7 ± 0.27 min incubating and made 1.0 ± 0.1 departures (range = 0–2) per 30-min watch. For all females (including those recorded on videotape), the average (continuous) duration of an incubation bout was 32.6 ± 3.5 min. After removing the effect of Julian day, the duration of incubation bouts was not significantly influenced by time of day, incubation day, or ambient temperature (Table 1). We detected no differences in incubation time between successful (i.e., surviving incubation or fledging at least one young) and unsuccessful nests (incubation: $t = 1.19$, df = 128, $P = 0.24$; fledging: $t = 0.089$, df = 128, $P = 0.93$; Fig. 1A).

Incubating females are faced with two decisions, the outcomes of which largely define incubation rhythms (Reid et al. 1999). The first decision—when to leave—is linked to female energy levels. The second—when to return—is linked to female foraging efficiency. In other words, on-bout duration is linked to

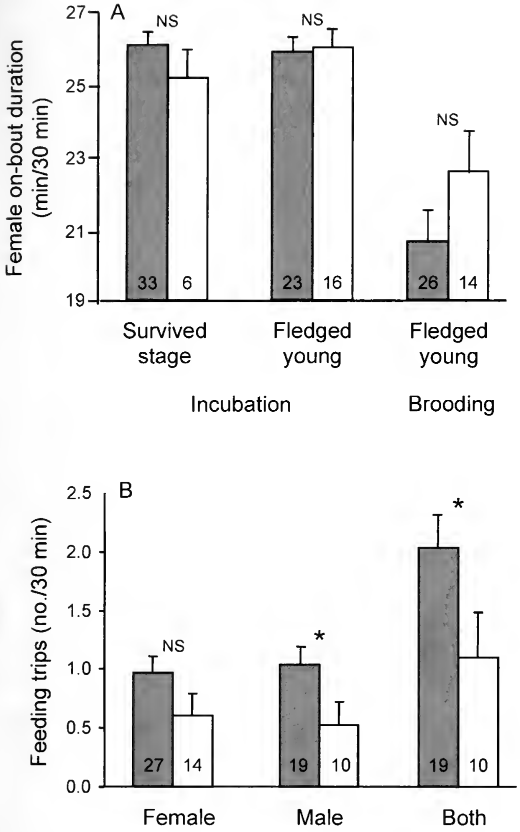

FIG. 1. Cerulean Warbler on-bout duration (A) and feeding behavior (B) for successful (filled bars) and unsuccessful (unfilled bars) nests, Queen's University Biological Station, eastern Ontario. For the incubation period, we defined success in two ways: first, whether or not the clutch hatched, and, second, whether or not at least 1 young fledged from the nest. For the brooding period, success was defined by whether or not at least 1 young fledged from the nest. Data for female on-bout duration and female feeding trips are from 1999 to 2001. Feeding trip data for male and sexes-combined are from 2000 to 2001. Values presented are means ± 1 SE with sample size inside each column. Brooding sample size is higher than incubation sample size as we included nests that were found after the eggs had hatched. Results of *t*-tests: NS = not significant, * = $P < 0.05$.

parental needs as much as it is to embryonic needs (Conway and Martin 2000a, b). That we detected no significant effect of ambient temperature on incubation patterns implies either (a) that the thermal needs of embryos were met by ambient temperatures (Webb 1987) on our study site, thereby releasing female behavior from this constraint during the day, or (b) that female behavior was constrained by other pressures, such as female condition, male behavior, or predation risk. Compared with other *Dendroica* warblers (Conway and Martin 2000b), we observed relatively infrequent female departures during incubation (Table 2). Given the lack of a significant relationship between incubation rhythms and temperature, this low frequency of nest departures may be indicative of a high risk of predation (Martin and Ghalambor 1999, Ghalambor and Martin 2002). Nest predation is likely the primary cause of nest failure on our study site (Jones et al. 2001), with Blue Jays (*Cyanocitta cristata*) being the primary predator (JJB pers. obs.); however, given the inaccessibility of most of our nests, we were unable to examine the contents of most abandoned nests to help confirm the cause of failure.

Brooding and feeding young.—Females spent 20.1 ± 7.84 min brooding and made 1.6 ± 0.2 departures (range = 0–3) per 30-min watch. For all females (including those recorded on videotape), the average (continuous) duration of brooding bouts was 16.2 ± 1.5 min. In both brooding models (Table 1), females tended to brood less as nestlings aged, but time of year, temperature, and male feeding rate had no significant effect. We detected no differences in time spent brooding for successful versus unsuccessful nests ($t = 1.63$, df = 104, $P = 0.11$; Fig. 1A).

Both males and females averaged 1.1 ± 0.1 feeding trips per 30-min watch (range: females = 0–3, males = 0–4). Females fed more frequently as nestlings aged and as male feeding rate increased (Table 3), corroborating the findings in previous studies (e.g., Nolan 1978, Conrad and Robertson 1993, Lozano and Lemon 1998, MacColl and Hatchwell 2003). Males ($t = 2.40$, df = 68 $P = 0.019$) but not females ($t = 0.85$, df = 93, $P = 0.40$; Fig. 1B) fed nestlings more often at successful nests than at unsuccessful nests. Adults (both sexes combined) at successful nests made approximately twice as many feeding trips per 30-min watch as they did at unsuccessful nests ($t = 2.12$, df = 68, $P = 0.038$; "Both" in Fig. 1B). While we have no direct evidence that differences in food-delivery rates were responsible for differences in nest success, a difference of 1 trip per 30-min watch is larger than it first appears. If we assume a 15-hr day,

TABLE 2. Parental behavior of *Dendroica* wood warblers of northeastern North America. A dash indicates behaviors for which we could find no published information. Very few quantitative estimates of mate feeding are available; therefore, we adopted the qualitative classification of Conway and Martin (2000b).

Species	Nest location	Incubation-bout length (min)	No. incubation departures (/hr)	Male incubation feeding	Nestling provisioning rate (/nest/hr)	Source
Bay-breasted Warbler (*D. castanea*)	Tree	18	5.5	Moderate	26	Griscom 1938, Williams 1996
Blackburnian Warbler (*D. fusca*)	Tree	21–22	4.2	Infrequent	—	Kendeigh 1945, Lawrence 1953, Morse 2004
Blackpoll Warbler (*D. striata*)	Tree	19	5.0	Moderate	3/nestling/hr	Bent 1953, Hunt and Eliason 1999
Black-throated Blue Warbler (*D. caerulescens*)	Shrub	20–31	2.9	Moderate	7	Kendeigh 1945, Holmes et al. 2005
Black-throated Green Warbler (*D. virens*)	Tree	50	1.9	—	12–14	Nice and Nice 1932a, b; Morse and Poole 2005
Cerulean Warbler (*D. cerulea*)	Tree	33	2.0	Infrequent	3–4	This study
Chestnut-sided Warbler (*D. pensylvanica*)	Shrub	23	4.5	Moderate	8	Kendeigh 1945, Lawrence 1948, Tate 1970, Richardson and Brauning 1995, Hanski et al. 1996
Magnolia Warbler (*D. magnolia*)	Tree	17	4.9	—	8	Hall 1994
Yellow Warbler (*D. petechia*)	Shrub	36	3.1	Frequent	—	Kendeigh 1945, Hanski et al. 1996, Goosen and Sealy 1982, Martin et al. 2000
Yellow-rumped Warbler (*D. coronata*)	Tree	—	—	—	8–10	Martin et al. 2000, Hunt and Flashpoler 1998

1 caterpillar/trip, 0.1 g/caterpillar, a 10-day nestling period, and 1 extra trip/30 min, parents at successful nests would have delivered approximately 30 g more food to nestlings than unsuccessful parents.

Because increased parental activity late in the nestling stage tends to increase predation risk (Martin et al. 2000), we find it surprising that parents at successful nests made more feeding trips than parents at unsuccessful nests; however, Cerulean Warblers feed nestlings at relatively low rates compared to other passerines (Martin et al. 2000; Table 2), which might lessen the predation resulting from increased activity. Taken together, our observations—male incubation feeding, low rates of female departure, low rates of food delivery, and the possible link between food provisioning and nesting success—suggest that Cerulean Warblers are tightly constrained by the competing pressures of predation risk and food provisioning.

ACKNOWLEDGMENTS

D. M. Aiama, R. D. DeBruyn, S. Harding, B. Risk, A. J. Stevens, and J. Vargas provided field assistance. Three anonymous reviewers made valuable contributions to the manuscript. The Queen's University Bio-

TABLE 3. Female Cerulean Warblers (temperature ANCOVA: n = 135 focal nest watches; male feeding-rate ANCOVA: n = 77) at the Queen's University Biological Station, eastern Ontario, 1999–2001, fed nestlings more as nestling aged and as their social mates fed more. No interactions were statistically significant (all $P > 0.10$). Boldface values denote significant model effects. The male feeding-rate model is based on 2000–2001 data only.

Source of variation	Mean square	df	F	P
Temperature as covariate (R^2 = 0.30)				
Time of day	0.19	1	0.19	0.67
Nestling age	2.77	12	2.77	**0.004**
Ambient temperature	0.05	1	0.05	0.82
Individual female	0.23	34	0.23	0.99
Error	1.00	68		
Male feeding rate as covariate (R^2 = 0.43)				
Time of day	0.68	1	0.81	0.37
Nestling age	1.68	11	2.01	0.051
Male feeding rate	7.52	1	9.01	**0.005**
Individual female	0.39	24	0.47	0.98
Error	0.84	39		

logical Station provided valuable logistical support. Wildlife Habitat Canada, the Eastern Ontario Model Forest Program, Natural Science and Engineering Research Council of Canada, and World Wildlife Fund of Canada (MacNaughton Conservation Scholarships, Endangered Species Recovery Fund), Queen's University, the Society of Canadian Ornithologists, and the American Ornithologists' Union provided financial support. This project is part of Natural Legacy 2000, a nationwide initiative in Canada to conserve wildlife in private and public habitats. We gratefully acknowledge the support of the Government of Canada's Millennium Partnership Fund.

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The Wilson Journal of Ornithology 118(3):326–332, 2006

COMPARATIVE SPRING MIGRATION ARRIVAL DATES IN THE TWO MORPHS OF WHITE-THROATED SPARROW

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ABSTRACT.—White-throated Sparrows (*Zonotrichia albicollis*) display a plumage dimorphism (*white-striped* and *tan-striped*) with attendant behavioral differences, including greater aggression levels in white-striped birds and negative assortative mating, in which tan-striped birds pair with white-striped birds. To determine whether morph influences migration timing, which could influence patterns of assortative mating, we evaluated the phenology of northbound migration among White-throated Sparrows from a long-term banding dataset collected at a southern Ontario banding station. White-throated Sparrows are sexed by wing-chord length, but there is an intermediate size for which sex cannot be assigned. When all birds were considered together (both known and unknown sexes, n = 6,243), the white-striped birds migrated earlier by slightly more than 2 days. The sexing criteria, however, appeared to yield a sample that was not representative of the whole population: when we included only birds for which sex was assigned (n = 2,794, 45% of all birds), white-striped birds apparently migrated earlier by more than 4 days, but separate analyses of males (n = 1,511) and females (n = 1,283) revealed no differences in migration timing between morphs. By measuring wing-chord lengths of internally sexed specimens (from the Royal Ontario Museum) collected during April to June (n = 273), we found that in both sexes the wings of white-striped birds were about 2% longer than those of tan-striped birds. When we used these specimen data to recalibrate the sexing criteria, (a) it was possible to assign sex to 1.47 times as many birds (n = 4,121; 66% of all birds), (b) sex ratios of the banded birds more closely approached what appears to be the natural sex ratio (approximately 1:1), and (c) within-sex analyses indicated that white-striped females migrate earlier than tan-striped females by about 1.3 days, whereas there was no statistical difference between male morphs in migration timing. *Received 25 April 2005, accepted 2 February 2006.*

The White-throated Sparrow (*Zonotrichia albicollis*) displays a plumage dimorphism (Lowther 1961) produced by an inversion in the second chromosome (Thorneycroft 1966). The two morphs are usually referred to as *white-striped* and *tan-striped*. The former has a gray breast and a bright white median crown stripe and supercilium, while the latter has a brown breast and a dull or tan-colored crown stripe and supercilium (Lowther 1961, Falls and Kopachena 1994). White-striped males are slightly heavier than tan-striped males and white-striped females, which are heavier than tan-striped females (Tuttle 1993). Thorneycroft (1975) showed that the nestling sex ratio was not significantly different from 1:1, and both morphs are represented nearly equally in adult populations (Falls and Kopachena 1994).

Ecological and behavioral differences between white-striped and tan-striped morphs include aggression levels, preferred breeding habitat, and patterns of parental care (e.g., Knapton and Falls 1982, 1983; Knapton et al. 1984; Kopachena and Falls 1993; Tuttle 1993; Falls and Kopachena 1994). In particular, white-striped males are most aggressive and tan-striped females are least aggressive (Kopachena and Falls 1993). Tuttle (2003) found that, compared to tan-striped males, white-striped males exhibited higher rates of attempted polygyny and intrusion into neighboring territories, and lower rates of parental care and mate guarding. Negative assortative mating occurs such that >95% of pairs comprise one bird of each morph (Lowther 1961, Falls and Kopachena 1994, Houtman and Falls 1994). It has been proposed that females of both morphs prefer tan-striped males, and that the negative assortative mating is facilitated, at least in part, by the ability of white-striped females to out-compete tan-striped females for tan-striped males (Houtman and Falls 1994).

Notwithstanding the lack of evidence demonstrating ratios that depart from 1:1 for sex or for morph, Falls and Kopachena (1994) found unequal numbers of the two types of breeding pair assortments in Algonquin Park, Ontario, with nearly 70% composed of white-striped males and tan-striped females. However, in another Algonquin Park study, Knap-

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ton and Falls (1982) found the ecological distribution of tan-striped males to be much broader than that of white-striped males. In addition, there is a male floater population that includes an unknown proportion of both morphs (Falls and Kopachena 1994).

Typical of males in migrant passerines, male White-throated Sparrows migrate earlier than females (Jenkins and Cristol 2002). Considering the higher aggression levels in both the male and female white-striped morph, earlier arrival times of white-striped birds at their breeding grounds would not be surprising. If white-striped males arrive before tan-striped males, they would have first choice of territory. If white-striped females arrive before tan-striped females, they would have first choice of males, allowing them to pair with the preferred tan-striped males. Thus, whether due to differences in latitudes of wintering ranges, different departure dates, or different rates of migration, timing of northbound (herein referred to as "spring") migration could represent one factor influencing negative assortative mating in this species.

Knapton et al. (1984) considered morph and sex when comparing arrival times of White-throated Sparrows at breeding territories in Algonquin Park. Their two-year study revealed no significant timing differences between male morphs, but there was an apparent difference among females, whereby white-striped birds arrived before tan-striped birds. They were reluctant to conclude whether white-striped females were actually migrating earlier or were merely detected earlier due to either their greater levels of aggression and vocal behavior or their earlier association with males.

Here, we report results of two independent, but related, investigations. We began by considering the issue of morph-specific migration timing. To do this, we used banding data from a bird observatory in southern Ontario to analyze passage dates of White-throated Sparrows during spring migration. We speculated that the apparent earlier arrival of white-striped females on the breeding grounds reflects real differences in migration timing; thus, we predicted that white-striped females pass through earlier than their tan-striped counterparts. When our results suggested problems with the sexing criteria (wing-chord length), we used museum specimens to investigate size differences between the two morphs to propose new morph-specific sexing criteria for the species. With these new rules, we reassigned sex to the birds in the banding data set and then repeated the analyses.

METHODS

Banding dataset.—We used White-throated Sparrow banding data collected at Long Point Bird Observatory (LPBO; 42° 35′ N, 80° 15′ W) on Lake Erie in southern Ontario. This species breeds north of LPBO, so passage times there were used as a proxy for arrival times at the nesting grounds. Observatory mist nets were opened on or near 1 April, prior to the mid-April arrival of the first White-throated Sparrows. Characteristics recorded at LPBO included wing-chord length, morph, weight, sex (by wing chord), date, and bander information.

Morph data were collected from 1981 through 1994, so we restricted our analysis to that period. We arbitrarily required a minimum of 25 individuals of each sex per spring migration to include that year's records in the dataset, which reduced the dataset to 6 years (1985–1986, 1991–1994). The White-throated Sparrow is dimorphic at least during spring migration and breeding (Atkinson and Ralph 1980, Falls and Kopachena 1994), which permitted morph assignment to 85% of the LPBO birds. Even though licensed banders train and supervise volunteers, non-assignment of morph probably was due to bander uncertainty in cases where birds with more intermediate plumage were caught. Furthermore, there may be instances in the datasets of incorrect morph assignment, although we think such mistakes would be unlikely during spring migration, when birds are in fresh plumage.

Following convention, the sexing technique used by banders at LPBO was based on wing-chord length (to the nearest mm) of the closed, unflattened wing chord, as measured from the most anterior point of the wrist joint to the tip of the longest primary. Birds of both morphs were sexed as male if the wing chord was ≥74 mm and as female if the wing chord was ≤68 mm. Birds with wing chords of 69–73 mm were designated as unsexed. We used chi-square analyses to determine whether the ratio of males to females in each morph differed from a 1:1 ratio. Julian dates were used for passage dates, and we followed convention by setting alpha levels at 0.05 and reporting means as ± SE.

Analysis of migration timing.—We conducted four one-way analysis of variance (ANOVA) in three analyses to determine whether white-striped and tan-striped birds arrived at different times and, if so, whether sex was a factor. We used all birds in the first analysis, pooling both sexed and unsexed birds ($n = 6{,}243$). In the second analysis, we used only sexed birds, but we pooled both sexes ($n = 2{,}794$). In the third analysis, we did not pool sexes so that we could examine migration phenology for males ($n = 1{,}511$) and for females ($n = 1{,}283$) separately.

Re-calibrating the sexing criteria.—Initial analyses (see below) indicated that using the established sexing criteria would not allow an impartial test of differences in migration timing between the two morphs. We surmised that there were slight size differences between the morphs that might be confounding the analyses. If true, using the established sexing criteria would result in samples that were not representative of the population. Because females are smaller than males, it seemed likely that if tan-striped birds were smaller than white-striped birds, the sexing criteria would bias designations of tan birds as female and white birds as male. Accordingly, we investigated the possibility of devising a more accurate, morph-specific sexing system by recalibrating the sexing criteria and then repeating the second and third analyses.

We obtained White-throated Sparrow skins ($n = 273$) from the Royal Ontario Museum (ROM) in Toronto, Ontario, Canada, to calibrate wing-chord length with sex and morph. Only birds collected during spring (April to June of each year) were used, and all specimens had been assigned sex based on examination of gonads rather than by wing chord. The length of the unflattened wing chord was measured three times for each bird, resulting in a mean measurement (to the nearest mm) that we used in our analysis. We used ANOVA to determine whether there was a within-sex difference in wing-chord length between white-striped and tan-striped birds.

We plotted wing-chord lengths of males and females, by morph, in a histogram to examine the range in overlap. We assumed a normal distribution within each sex of the ROM specimens. By convention, we accepted a two-tailed alpha level of 0.05, which allowed error rates of 2.5% on the upper end of the females' distribution and on the lower end of the males' distribution. These measurements were used to set new morph-specific measurements of wing-chord length for sexing the birds.

To determine whether the morph-specific sexing criteria yielded fewer unsexed birds, we used a one-sample sign test to compare the tallies of male, female, and unsexed birds assigned via the new criteria to those assigned via the established criteria. Specifically, we wished to see whether the new criteria increased numbers of white-striped females and tan-striped males. Chi-square analysis was used to determine whether the ratio of males to females in each morph differed from 1:1 after the proposed sexing criteria had been applied to the LPBO dataset. Once we determined that the morph-specific sexing criteria were superior, as demonstrated by substantial increases in sample sizes, we applied them to the LPBO data. Because we expected migration passage to be normally distributed (Mills 2005), we expected the distribution of accumulated percentages of migrants to be sigmoid; thus, we applied a third-order polynomial model to our distributions. Once such curves were estimated from the data, we compared morph passage times by comparing respective areas under morph-specific curves by using integrals.

RESULTS

Migration phenology using the established sexing criteria.—White-striped birds slightly outnumbered tan-striped birds in the banding dataset (56% white-striped). Using all banded birds for which morph was assigned ($n = 6{,}243$), there was a significant difference in the arrival times of the two morphs ($F_{1,6241} = 119.7$, $P < 0.001$). White-striped birds arrived 2.15 days earlier than the tan-striped birds (white-striped CI: 0.25 days; tan-striped CI: 0.30 days).

Using the established sexing criteria, only about 45% of the birds were sexed, and there were significantly fewer white-striped birds sexed as females than as males ($n = 1{,}561$, 29% female; $\chi^2 = 279.9$, df = 1, $P < 0.001$)

TABLE 1. Number of male, female, and unsexed White-throated Sparrows of both tan-striped and white-striped color morphs, identified according to established and re-calibrated sexing criteria. Birds were captured and banded at the Long Point Bird Observatory (LPBO), Long Point, Ontario (6 years: 1985–1986, 1991–1994).

	White-striped birds				Tan-striped birds			
	Established		Proposed		Established		Proposed	
Sex	*n*	Percent	*n*	Percent	*n*	Percent	*n*	Percent
Female	450	13.0	760	21.9	833	30.0	833	30.0
Male	1,111	32.0	1,560	45.0	400	14.4	968	34.9
Unsexed	1,909	55.0	1,150	33.1	1,540	55.5	972	35.1
Total	3,470				2,773			

and significantly more tan-striped birds sexed as females than as males (n = 1,233, 68% female; $\chi^2 = 152.1$, df = 1, $P < 0.001$). Furthermore, the apparent migration timing differences between morphs were exaggerated when only sexed birds were pooled and analyzed, with white-striped birds apparently migrating 4.27 days earlier than the tan-striped birds ($F_{1,2792} = 192.7$, $P < 0.001$). Finally, when separate analyses were conducted for males and females, apparent differences in migration timing between morphs were <1 day in both cases, and neither was statistically significant (males: $F_{1,1509} = 2.71$, $P = 0.10$; females: $F_{1,1281} = 3.19$, $P = 0.074$). Accordingly, we concluded that the sexed samples were neither reliable nor representative of the population, and we resorted to museum skins to see whether more reliable sexing criteria could be employed.

Re-calibrating the sexing criteria.—Analysis of the ROM skins showed that the wing chords of white-striped females (n = 46; 68.93 mm ± 0.63) significantly exceeded those of tan-striped females (n = 55; 67.61 mm ± 0.65) by an average of 1.32 mm ($F_{1,99} = 8.30$, $P = 0.005$). The difference in male wing-chord lengths was also significant ($F_{1,170} = 25.8$, $P < 0.001$), with those of white-striped birds (n = 99; 73.31 mm ± 0.43) averaging 1.48 mm longer than those of tan-striped birds (n = 73; 71.84 mm ± 0.34). In both sexes, the average wing-chord length of white-striped morphs was ~2% greater. Using the new sexing criteria and accepting a 2.5% error rate, we determined that we could not assign sex to white-striped birds with wing-chord lengths of 70–72 mm, nor to those of tan-striped morphs with wing-chord lengths of 69–71 mm.

When we reapplied the revised sexing criteria to the LPBO data and conducted a one-sample sign test on the data, 1.47 times as many birds were sexed, a significant increase (white-striped: n = 3,470, df = 1, $P < 0.001$; tan-striped: n = 2,773, df = 1, $P < 0.001$). In addition, sex ratios were less skewed for both morphs: the percentage of females increased modestly among white-striped birds (29% to 33%) and decreased dramatically among tan-striped birds (68% to 46%; Table 1). In both morphs, however, sex ratios still differed from a 1:1 ratio (white-striped: n = 2,320, $\chi^2 = 275.9$, df = 1, $P < 0.001$; tan-striped: n = 1,801, $\chi^2 = 10.1$, df = 1, $P = 0.001$).

Using the new sexing criteria, we repeated the second ANOVA by pooling males and females for both white- (n = 2,320) and tan-striped (n = 1,801) morphs and comparing phenologies by morph. White-striped birds passed LPBO 2.06 days earlier than tan-striped birds ($F_{1,4119} = 67.7$, $P < 0.001$). Accordingly, we concluded that the samples sexed by using the new sexing criteria were representative of the whole population, because 2.06 days (calculated using only sexed birds) is very close to 2.15 days (calculated using all birds) and substantially different from the 4.27-day difference in migration timing (calculated using only birds sexed with the established sexing criteria).

Migration phenology using the re-calibrated sexing criteria.—Being satisfied with the new sexing criteria, we repeated the third analysis by comparing the within-sex passage dates for both morphs. Progression of the spring passage for the four sex-morph classes of White-throated Sparrow at LPBO is shown in Figure 1. As expected, third-order polyno-

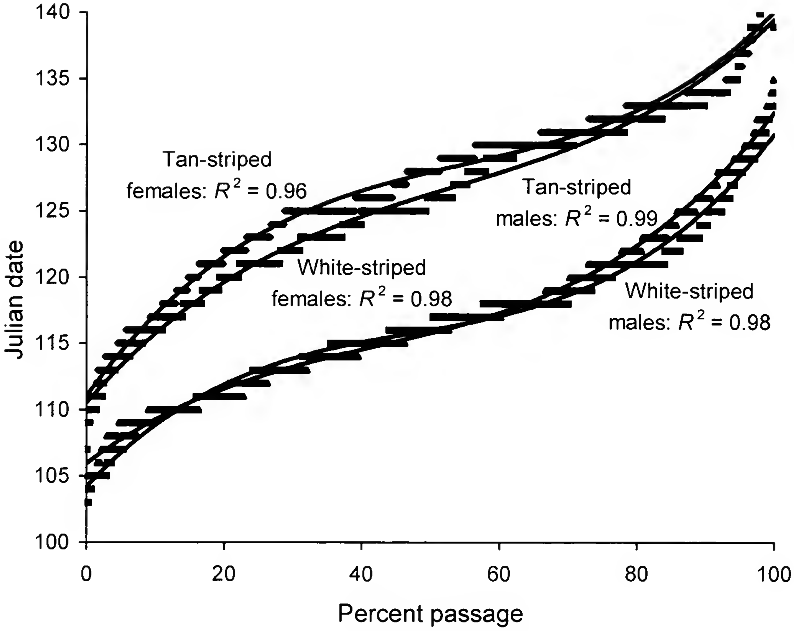

FIG. 1. Progression of spring (northbound) migration among sexes (females: the two upper curves; males: the two lower curves) and color morphs of White-throated Sparrows caught and banded at Long Point Bird Observatory, Long Point, Ontario. Birds were identified on the basis of sex and morph using re-calibrated sexing criteria (see text). The curves represent 3rd-order polynomials that describe the timing of each group's passage (R^2 values range from 0.96 to 0.99). For each curve, bar widths represent the proportion of birds passing through on each particular Julian date. Compared with tan-striped females, passage was significantly earlier for white-striped females (n = 1,593, $F_{1,1591}$ = 13.8, $P < 0.001$) by about 1.3 days; there was no difference in arrival time of male morphs (n = 2,528, $F_{1,2526}$ = 2.25, P = 0.13). Tan-striped females took 7% longer than white-striped females to complete their migration (see text).

mials described the migration timing well, with the four R^2 values ranging from 0.96 to 0.99. Using the 1st day of female migration as time zero and calculating the areas under each such curve by using integrals, tan-striped females took 7% longer than white-striped females to complete their migration. On average, this amounted to a significantly later arrival (1.3 days, n = 1,593, $F_{1,1591}$ = 13.8, $P <$ 0.001). Likewise, the passage of tan-striped males was 2.6% longer than that of white-striped males (n = 2528, $F_{1,2526}$ = 2.25, P = 0.13).

DISCUSSION

Several studies of aggression levels among white-striped and tan-striped morphs in White-throated Sparrows revealed that both sexes of the white-striped morph appear to be more aggressive than their tan-striped counterparts (e.g., Watt et al. 1984, Kopachena and Falls 1993, Collins and Houtman 1999). To this body of knowledge we add the observation that white-striped females arrive at the breeding grounds earlier than tan-striped females. Our results are consistent—for both male and female arrival dates—with those of Knapton et al. (1984), who detected (a) white-striped males slightly, but not significantly, earlier than tan-striped males, and (b) white-striped females significantly earlier than tan-striped females. Results of our study, however, point to real differences in female migration timing, rather than differences in detections of white-striped and tan-striped birds.

Since male arrival dates are similar for both morphs, perhaps it is the earlier arrival of white-striped females that facilitates the negative assortative mating in this species. This is consistent with the mechanism proposed by Houtman and Falls (1994), whereby white-striped females out-compete tan-striped females for the tan-striped males. We suggest, however, that dominance does not act alone;

rather, the morph-specific migration phenologies also give a competitive advantage to white-striped females. While the 1- to 2-day difference in timing that we report here is modest, it is not implausible that it is sufficient to confer on white-striped females a competitive advantage over their tan-striped counterparts.

Early arrival can confer a higher social status in migrant birds (e.g., Red-winged Blackbirds, *Agelaius phoeniceus*; Cristol 1995). In White-throated Sparrows, Watt et al. (1984) concluded that the dominance between female morphs is seasonally dependent, whereby white-striped females are dominant on the breeding grounds and the tan-striped females are dominant on the winter grounds. The earlier spring arrival of white-striped females may then represent the switch in social status between female morphs. Inferior social status on the winter grounds could mean that the best strategy for white-striped females is to leave earlier in spring to attain a higher social status than tan-striped females. Others have concluded, however, that morph type has no effect on social rank in winter (Piper and Wiley 1989).

Alternatively, we acknowledge the possibility that the earlier arrival of white-striped females demonstrated in our study is merely facilitated by their larger size and may have no functional significance in negative assortative mating or dominance relationships. We think this unlikely, however, because white-striped males are bigger than tan-striped males, and yet their migration phenologies do not differ.

Because white-striped females exhibit lower levels of parental care than tan-striped females in normal, two-parent nests, Knapton and Falls (1983) questioned the ability of white-striped females to raise broods on their own without a mate. If true, fledging success among white-striped females might be enhanced if they pair with tan-striped males, as the latter exhibit parental contributions that match those of white-striped females and exceed those of white-striped males (Knapton and Falls 1983). In another study, however, Whillans and Falls (1990) found that both white-striped and tan-striped females compensate in terms of parental care when males are removed from the nest, and both female morphs are able to successfully fledge young. Whillans and Falls (1990) suggested that the difference in results between the two studies might be explained by differences in study sites that supported differing densities of white-striped males.

Previously, researchers have suggested that nearly 70% of all White-throated Sparrow pairs are composed of white-striped males and tan-striped females (Thorneycroft 1975, Knapton and Falls 1983). This is perplexing, since the nestling ratio and the banding data we present suggest that the morph ratio is much closer to 1:1. It is not known whether tan-striped birds are predominant among populations of floating males, or whether white-striped birds are predominant among populations of non-breeding females. White-striped birds are more conspicuous compared to their tan-striped counterparts in song, territorial behavior, and overall brightness in color (Lowther 1961, Falls and Kopachena 1999), and this may influence apparent proportions of pair-assortment types.

With white-striped birds being larger and having significantly longer wing chords, we feel it would be logical to use two sexing systems when wing-chord length is employed. Rising and Shields (1980) found that, generally, tan-striped males were slightly smaller overall than white-striped males, and that generally white-striped females were larger than tan-striped females in terms of most characteristics that they measured. To assist in more comprehensive sex assignment and to generate samples more accurately representing natural populations, we suggest that these new sexing criteria be used whenever morph identification is possible. Although the sexing criteria proposed here yielded only slightly different wing-chord lengths than those measured by the established sexing criteria, implementing this change substantially increased the number of birds to which we could assign sex. When morph identification is not possible, the established wing-chord rule, as suggested in Pyle (1997), should be used.

Previously, it was known that there are several differences between white-striped and tan-striped morphs of White-throated Sparrows, including size, habitat, aggression levels, and parental care (Rising and Shields 1980, Knapton and Falls 1982, Houtman and

Falls 1994). Our study reveals yet another difference: the timing of spring migration among females differs between morphs. Overall, it appears that the White-throated Sparrow's morph-based systems of migration timing and social structure are unique among passerine birds.

ACKNOWLEDGMENTS

We are grateful to the many volunteers of the Long Point Bird Observatory (LPBO), as well as J. D. McCracken (LPBO—Bird Studies Canada), for providing us with the raw data. We also thank M. K. Peck at the Royal Ontario Museum for allowing us access to White-throated Sparrow skins. J. D. Rising provided support and helpful comments throughout the project, and J. B. Falls and two anonymous reviewers provided invaluable suggestions that improved the manuscript.

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The Wilson Journal of Ornithology 118(3):333–340, 2006

CAN SUPPLEMENTAL FORAGING PERCHES ENHANCE HABITAT FOR ENDANGERED SAN CLEMENTE LOGGERHEAD SHRIKES?

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ABSTRACT.—Habitat degradation caused by feral grazers has been identified as a possible limiting factor for the endangered San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*). In 1999, we installed supplemental foraging perches within shrike breeding territories on San Clemente Island and observed shrike foraging behavior before and after perches were installed. Shrike foraging efficiency, determined by measuring foraging attack distances and success rates, was not improved when supplemental perches were present; however, shrikes shifted their focal foraging sites to areas where perches were installed. Shrike home ranges did not change size when supplemental perches were installed, indicating that foraging areas made available by adding supplemental perches were not of higher quality than those that were previously available. However, the addition of supplemental perches may have increased the total foraging habitat available to this endangered subspecies. *Received 13 May 2005, accepted 17 February 2006.*

Habitat deficiencies have been identified as possible limiting factors in populations of Loggerhead Shrikes (*Lanius ludovicianus*; Yosef 1994, Cade and Woods 1997). In the 1980s, Scott and Morrison (1990) studied a population of endangered shrikes on San Clemente Island (SCI), the San Clemente Loggerhead Shrike (*L. l. mearnsi*). In the late 1890s and early 1900s, Grinnell (1897) had considered this subspecies "tolerably common; that is, two or three could generally be seen during an hour's walk," and Linton (1908) called the population "fairly well distributed." By the 1990s, the population on SCI had dropped to a low of 13 individuals (T. Mader unpubl. data). Scott and Morrison (1990) identified habitat degradation attributed to overgrazing by feral goats (*Capra hircus*) as a likely cause of this subspecies' decline. Common effects of overgrazing by feral goats include depletion of woody species and an increase in exotic vegetation (Coblentz 1980).

Because shrikes use elevated substrates as foraging perches, from which they can readily see prey and attack with flights to the ground (Bent 1950), perches are an important component of shrike territories (Esely and Bollinger 2001). If elevated perches are lacking, shrikes may not be able to use all potential foraging habitat and may, therefore, increase their home-range size to encompass an adequate area of usable habitat. Having to move about larger home ranges and defend larger territories requires that shrikes expend greater amounts of energy; this may result in a decrease in their nutritional status (Yosef and Grubb 1992). The establishment of larger territories also decreases the shrike carrying capacity of SCI's limited area. Yosef and Grubb (1994) found that adding fence posts to shrike territories in Florida resulted in smaller average territory sizes and greater breeding densities of shrikes. Artificial perches have also been shown to attract raptors, especially kestrels (*Falco* sp.), to areas that were otherwise devoid of appropriate perches (Kay et al. 1994, Wolff et al. 1999, Kim et al. 2003).

Optimal foraging theory suggests that an animal will optimize the capture and consumption of prey, maximizing energy intake while minimizing energy expenditure (Schoener 1971, Mills 1979). Therefore, an increase in foraging efficiency should be reflected by shorter attack distances (less energy required to fly a shorter distance), capture of larger prey items (fewer attempts needed), and a greater percentage of successful foraging attempts (less wasted energy on failed foraging attempts). An increase in foraging efficiency also may be reflected by more frequent captures per unit time, even if success rate does not improve. Furthermore, shrikes may select nest locations near foraging areas to decrease energy expended in flight while tending a nest.

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Shrike foraging efficiency may be constrained by the number and arrangement of available hunting perches. Prior to our supplemental perch experiment, we had found a greater number of trees and shrubs at sites occupied by shrikes on SCI than at sites shrikes had abandoned within the past 10 years (SL unpubl. data). If hunting perches are limited, then it seemed reasonable to expect that the addition of supplemental perches within shrike territories would allow foraging efficiency to increase by providing shrikes a greater choice of hunting perches, thereby increasing their opportunity to choose the best hunting area. Therefore, we designed an experiment to determine whether the addition of supplemental perches to shrike territories would increase foraging efficiency and the effective usable area of a given home range. We also examined whether the presence of supplemental perches would alter shrike breeding behavior by allowing them to forage nearer to their nests.

METHODS

Study area.—San Clemente Island (32° 50′ N, 118° 30′ W), the southern-most of California's Channel Islands, is located about 100 km northwest of San Diego, California. The island is 28 km long (width = 3–7 km, area = 145 km^2) and rises abruptly to 599 m in elevation on the eastern escarpment. Numerous canyons cut through marine terraces on the southwestern part of the island. Island temperatures range from 7–35° C, precipitation ranges from 12–20 cm/year (mainly November through March), and fog is common, especially in summer months (Jorgensen and Ferguson 1984, Scott and Morrison 1990).

Native vegetation on the island has been substantially altered by introduced herbivores, including sheep (*Ovis aries*), goats, and pigs (*Sus scrofa*), all of which were eradicated by 1993. By the time of our study, the dominant plant community comprised native and nonnative grasses (including *Avena*, *Bromus*, and *Nassella* spp.) interspersed with areas of recently recruited coyote brush (*Baccharis pilularis*), which covered ~33% of the flatter upper reaches of the island (U.S. Department of the Navy 2001). Shrubs and trees were primarily restricted to the canyon bottoms. SCI is operated by the U.S. Navy as a training base, primarily for ship-to-shore bombardment in the area where we conducted our study. See U.S. Department of the Navy (2001) for additional information on the island's vegetation, geography, and other natural resources.

Site selection and study design.—In 1999, we selected four (of eight total) pairs of breeding shrikes on SCI for study. None of the pairs' home ranges overlapped, and the distance between the edge of each pair's home range and its closest neighbor ranged from 100–800 m. Sample size was constrained by logistical and conservation considerations, such as site accessibility and concerns about manipulating the breeding sites of a highly endangered population. We studied shrike behavior and recorded their responses to supplemental perches during two periods: 13 March through 4 June (period 1) and 5 June through 2 August 1999 (period 2). On 13 March, we installed supplemental perches at two sites (A and D; Fig. 1). During period 1, we observed at least 75 foraging attempts at the sites with supplemental perches and also at two sites (B and C; Fig. 1) without supplemental perches. On 5 June, we removed the perches from sites A and D and installed them at sites B and C; during period 2, we observed another 75+ foraging attempts at each site. This paired sampling design controlled for seasonal and individual differences in behavior.

The shrike breeding season typically begins in January with pair formation and extends through mid-August, when the last fledglings disperse from their natal territories. Because we were concerned that different breeding stages might elicit differences in foraging behavior, we recorded the shrikes' breeding stage throughout the study and mapped the locations of their nests. During the nestling and fledgling stages, shrikes may alter their foraging behavior by increasing foraging rates to provide for their young. Therefore, we eliminated foraging attempts observed during these periods to avoid biasing our results.

At sites B and C, the original females were replaced by captive-released females during the breeding season. The original female at site B disappeared between 11 and 17 April and was replaced with a released female on 1 May. We collected data on this female during both study periods. At site C, the original fe-

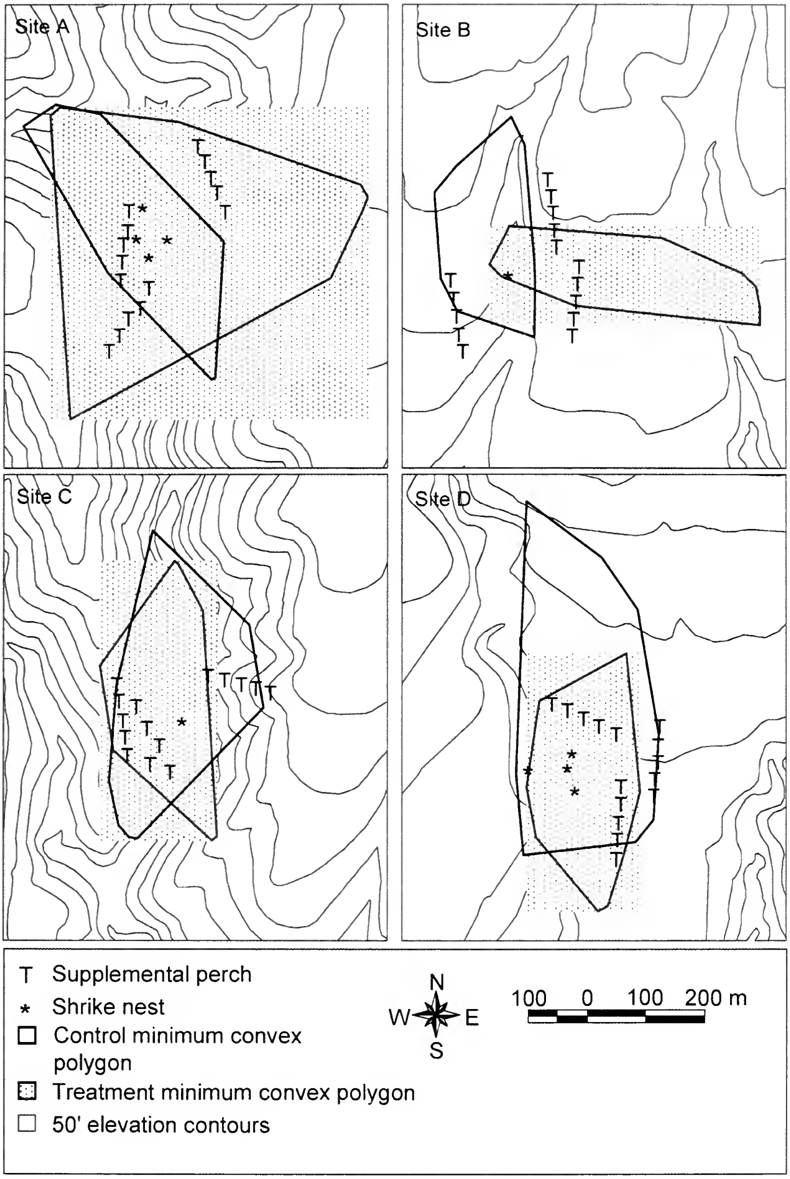

FIG. 1. Maps of minimum convex polygon home-range estimates, encompassing all foraging locations, when supplemental perches were present (treatment) and not present (control) within San Clemente Loggerhead Shrike territories, San Clemente Island, California, 1999.

male was depredated between 2 and 5 May and replaced with a released female on 15 May, prior to the installation of supplemental perches at that site.

At all sites, we installed 3 groups of 5 supplemental perches, arranged linearly where possible (Fig. 1), for a total of 15 perches per site. Within a group of five, we spaced supplemental perches 30 m apart, which was twice the average attack distance for a ground foraging attempt (SL unpubl. data), and >30 m from naturally occurring, elevated (>2 m) perches. We placed each line of perches at a randomly selected distance (1 to 200 m) from the shrike activity center at each site, and we oriented each line according to randomly selected compass directions. Supplemental perches were poles of aluminum conduit (3 m long, 1.3 cm in diameter) slipped over a piece of rebar pounded into the ground. Attached to each pole were three horizontal cross pieces (40 cm long) made of wooden dowels (0.3 cm in diameter) positioned at 2.5, 1.5, and 0.75 m from the ground. Barbed wire was wound around the joint of the cross piece and upright conduit to serve as a site for shrikes to impale their prey.

Data collection.—We identified all shrikes by unique combinations of colored leg bands. Our observation points were >50 m away from the center of shrike activity to avoid disturbing the shrikes; at sites where one observation point was not sufficient to observe the entire area, we placed additional points at variable distances from the activity center. We observed each shrike pair for 0.5–1.0 hr per visit. In addition to bird identity and weather conditions, for each foraging attempt we recorded perch substrate, perch height, type of foraging maneuver (aerial sally, ground forage [flight to the ground from an elevated perch], or vegetation glean), outcome, foraging-attempt distance, and prey captured (mouse, lizard, bird, small arthropod [≤10 mm, i.e., smaller than the length of a shrike bill], and large arthropod [>10 mm]). Because there were significant differences between male and female behaviors (i.e., the female is the primary incubator, the male provisions the female when she is on the nest), we analyzed foraging behavior separately by sex.

Statistical analyses.—We mapped the locations of perches used by shrikes during foraging attempts, then transferred these locations to ArcView, v. 3.2a (Environmental Systems Research Institute, Inc. 2000). We generated minimum convex polygons using ArcView Animal Movements Extension, v. 2.0 beta (Hooge et al. 1999) for locations mapped when supplemental perches were present (treatment: n = 73–85) and not present (control: n = 80–94). We used paired t-tests to compare the sizes of minimum convex polygons between treatments and controls. To determine whether shrikes shifted their foraging areas in response to the installation or removal of supplemental perches, we also mapped the locations of supplemental perches used by shrikes and then counted the number that fell within the polygons generated during treatment and control periods. We used Fisher's exact test of independence (Sokal and Rohlf 1981) to compare the number of perch sites used during control and treatment periods.

To determine whether supplemental perches affected the selection of nest sites, at each site we recorded whether each nest was initiated during treatment or control. For nests initiated during treatment, we measured the distance from the nest to all supplemental perches. For nests initiated during control, we measured the distance from the nest to where the supplemental perches were installed during treatment. At sites where shrikes built nests during both treatment and control, we compared the mean nest-to-supplemental perch distance during treatment to the mean nest-to-supplemental perch distance for all supplemental perch sites (i.e., perch site = location where a supplemental perch would be, or had been, placed during treatment) during control. We used paired t-tests to ascertain differences in foraging-attempt distances between treatment and control. Where sample sizes were large enough, we used chi-square tests to test for treatment versus control differences in forage-maneuver type, foraging success, and size of prey item captured; otherwise we used Fisher's exact test. Because of inherent differences in foraging-maneuver type (i.e., larger prey items, such as lizards and mice, were not captured during aerial sallies), we analyzed size of prey and foraging-attempt distances by type of foraging maneuver. Means are reported ± SD. We considered $P \leq 0.05$ to be statistically significant.

RESULTS

We observed a total of 674 foraging attempts, 338 of which occurred during the treatment phase (110 from supplemental perches, 228 from naturally occurring perches) and 336 during the control phase of our study. After eliminating foraging attempts when nestlings or fledglings were present, we were able to determine whether a foraging attempt was successful for 447 attempts, 224 during treatment (86 from supplemental perches and 138 from naturally occurring perches) and 223 during control.

Pairs at sites B and C built and tended one

TABLE 1. Distance between nests and supplemental perches installed within San Clemente Loggerhead Shrike territories, San Clemente Island, California, 1999. During control periods, distances were measured between nests and the pre-designated locations of supplemental perches, which were present only during treatment periods.

Site	Nest	Period when nest initiated	Distance to nearest supplemental perch	Mean distance (± SD) to supplemental perches
A	A	Pre-study	41 m	118 ± 52 m
	B	Treatment	31 m	153 ± 63 m
	C	Control	121 m	274 ± 97 m
	D	Control	132 m	233 ± 68 m
B	A	Control	70 m	149 ± 61 m
C	A	Control	72 m	122 ± 35 m
D	A	Pre-study	80 m	119 ± 29 m
	B	Treatment	73 m	121 ± 27 m
	C	Control	111 m	145 ± 29 m
	D	Control	85 m	126 ± 31 m

nest each. Shrike pairs at sites A and D, however, each built and tended four consecutive nests, none of which were successful. One nest at each of these two sites was initiated during treatment (i.e., supplemental perches were present). Both of the nests initiated during treatment were closer to the nearest supplemental perch site than any other nests (Table 1). The mean distance from each of these two nests to all supplemental perch sites, however, was not shorter than that of nests initiated when supplemental perches were not present (Table 1). Shrike home-range size did not differ between treatment and control (treatment: 8.5 ± 6.1 ha; control: 7.7 ± 2.7 ha; t_3 = 0.24, P = 0.83). However, shrikes shifted their home ranges to include some of the supplemental perches when they were present. Significantly more of the supplemental perch sites were located within shrike home ranges during treatment (n = 40) than during control (n = 32; P = 0.023, df = 3).

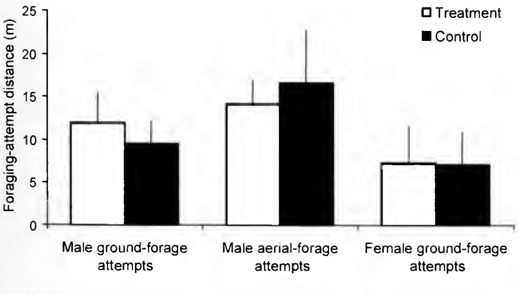

FIG. 2. Mean ± SD foraging-attempt distances of male and female San Clemente Loggerhead Shrikes in territories with (treatment) and without (control) supplemental perches, San Clemente Island, California, 1999.

The addition of supplemental perches did not affect average distance of foraging attempts (Fig. 2). For male shrikes, attack distances for ground-foraging attempts were not affected by the presence of supplemental perches (n = 300, t_3 = 1.06, P = 0.37) nor were attack distances of aerial sallies (n = 140, t_3 = 0.59, P = 0.60; Fig. 2). Likewise, female attack distances for ground-foraging attempts were not affected by the presence of supplemental perches (n = 51, t_2 = 0.29, P = 0.79). We did not observe a sufficient number of vegetation gleans for analysis of attack distance. Also, the addition of supplemental perches did not result in altered proportions of foraging maneuver types used by males (n = 471, χ^2 = 0.48, P = 0.79, df = 2) or females (n = 70, χ^2 = 2.68, P = 0.10, df = 1; Fig. 3).

Foraging success of neither males (n = 327, χ^2 = 1.53, P = 0.22, df = 1) nor females (n = 52, χ^2 = 0.79, P = 0.38, df = 1) improved when supplemental perches were present (Fig. 4). Shrikes foraged from supplemental perches 33% of the time when they were present, and we found no difference in the proportion of successful foraging attempts launched from supplemental and naturally occurring perches (n = 224, χ^2= 1.43, P = 0.23, df = 1). Although shrikes tended to capture more prey/hr when using supplemental perches (0.98 ± 0.48 successful foraging attempts/hr) than when using naturally occurring perches (0.52

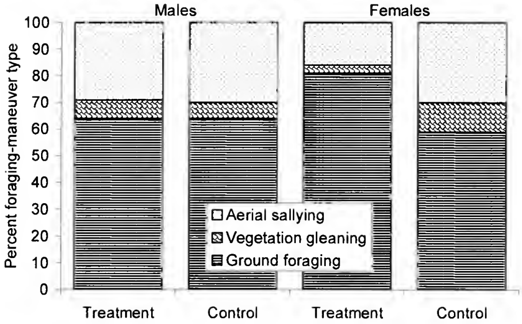

FIG. 3. Percentages of foraging-maneuver types performed by San Clemente Loggerhead Shrikes in territories with (treatment) and without (control) supplemental perches, San Clemente Island, California, 1999.

± 0.15), the difference was not significant ($n = 159$, $t_3 = 1.84$, $P = 0.16$). Shrikes always perched on the top-most crossbar before foraging, and only once did a shrike use a lower crossbar—briefly, before moving up to the top crossbar.

During ground-foraging attempts, neither males ($n = 95$, $\chi^2 = 1.46$, $P = 0.23$, df = 1) nor females ($n = 14$, Fisher's exact $P = 0.46$, df = 1) captured larger prey (small/large: males with supplemental perches = 33/19, males without supplemental perches = 22/21, females with supplemental perches = 2/2, females without supplemental perches = 7/3) when supplemental perches were present. During aerial sallies, however, males captured more small arthropods than large arthropods when supplemental perches were present ($n = 93$, Fisher's exact $P = 0.007$, df = 1; small/large: with supplemental perches = 43/3, without supplemental perches = 34/13). Vegetation gleans by males tended to yield smaller prey when supplemental perches were present ($n = 22$, Fisher's exact $P = 0.08$, df = 1; small/large: with supplemental perches = 8/5, without supplemental perches = 2/7).

DISCUSSION

Although many aspects of shrike foraging efficiency did not increase when we installed supplemental perches, San Clemente Loggerhead Shrikes responded positively to the presence of supplemental perches by increasing their use of the areas around the perches. Shrikes readily used supplemental perches, and we found that when supplemental perches were added to a home range, shrikes shifted their foraging habitat to include the area around some, but not all, of the supplemental perches. The one exception to this pattern was an apparent shift toward an area without supplemental perches that was burned by a late-season fire at site B.

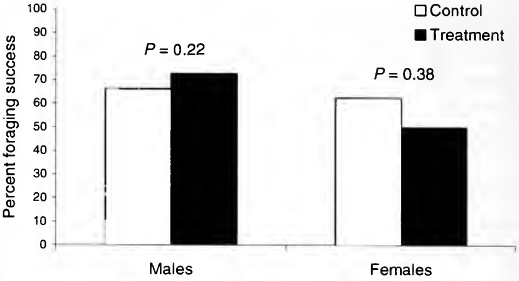

FIG. 4. Percent foraging success of male and female San Clemente Loggerhead Shrikes in territories with (treatment) and without (control) supplemental perches, San Clemente Island, California, 1999.

The shift in areas used by shrikes when supplemental perches were present suggests that some areas of the shrikes' home ranges contained prey resources that could not be used due to a lack of appropriate foraging perches. Although our sample size was insufficient for statistical comparisons, the shrikes seemed to place their nests closer to supplemental perches when they were present (Fig. 1); if true, shrikes may have reduced their energetic costs by taking advantage of the newly available foraging areas. Tall perches may have provided other benefits to shrikes, including increased capacity for predator vigilance and more display areas for territory defense and mate attraction. In contrast, Chavez-Ramirez et al. (1994) found that shrikes in natural grasslands in Texas did not shift their foraging areas as densities of artificial perches were manipulated; instead, the shrikes increased their use of herbaceous perches, and Chavez-Ramirez et al. (1994) concluded that foraging perches were not a limiting factor in natural grasslands.

Habitat enhancement has yielded beneficial results where focal species lacked certain habitat components. In disturbed landscapes of Washington state (Rocklage and Ratti 2000), bird species diversity increased with the addition of irrigation along the Snake River and, in New Zealand, several bird species increased their use of areas cleared of willows along braided rivers (Maloney et al. 1999). Probably due, in part, to the extremely low number of shrikes on SCI, we did not see a similar increase in bird density with the addition of supplemental perches. Consequently, the lack of intraspecific competition between San Clemente Loggerhead Shrikes allowed them to investigate areas that were previously unavailable and to respond opportunistically to novel structures. We did not find a concurrent increase in foraging success or efficiency with the addition of supplemental perches, indicating that the areas opened up for foraging by the addition of perches may not have been superior to those already available. This idea was supported by the substantial overlap in areas used during treatment and control periods (Fig. 1) and our observation that shrikes did not use all of the supplemental perches provided, both of which indicate that the habitat quality in some areas was poor and would not be enhanced even by the installation of supplemental perches.

Shrikes in Florida reduce their territory size with the addition of foraging perches, and new shrike pairs will establish territories in the areas vacated (Yosef and Grubb 1994). When a limited resource (foraging perches) is added, shrikes are able to decrease the energy expended on moving throughout and defending a large territory from other shrikes, thereby potentially improving their nutritional status (Yosef and Grubb 1992). With the decrease in territory size defended, and the density increase in pairs of shrikes, the addition of supplemental perches potentially increased the carrying capacity of shrike habitat in Florida.

Unlike shrikes in Florida, however, home-range size of San Clemente Loggerhead Shrikes was not affected by the presence of additional foraging perches. On SCI, the low number of breeding shrikes (eight pairs) negated the advantage of decreasing home-range size to reduce energy expenditure on territory defense. Shrike home-ranges were far enough apart (>100 m; T. Mader unpubl. data) that territorial defense against neighboring shrike pairs was unlikely to limit the home-range size of the resident pair. Furthermore, because the shrike population in our study was thoroughly observed and color-marked, we are confident that no additional shrike pairs were breeding nearby; therefore, little competition for breeding resources could have occurred.

After the addition of supplemental perches, San Clemente Loggerhead Shrikes incorporated previously unused habitat while maintaining similarly sized home ranges, suggesting that other aspects of their home range were still important to their survival. Supplemental perches provided substrates on which to perch and impale captured prey, but did not provide the structure and foliage of trees—features required by shrikes for nest placement and for concealment and escape from predators. Kim et al. (2003) found that shrikes were more closely associated with natural woody perches than artificial perches and attributed this association to the lack of escape cover at artificial perches. In Kansas, the number of potential nesting trees was the most important predictive variable for shrike habitat suitability (Lauver et al. 2002). Trees and shrubs on SCI can attain heights of >10 m, but they are limited to canyon bottoms and other areas that were protected from goat herbivory. Nonetheless, shrikes must include these remnant trees and shrubs in their breeding home ranges for successful reproduction and survival.

In contrast to Yosef and Grubb (1994), we did not find evidence that the availability of suitable foraging perches limits shrikes energetically, possibly due to the differences in terrain between their study site and ours. Shrikes on SCI typically inhabit steep, rocky, topographically complex canyons, although they occasionally forage on flat mesas between canyons. In such topographically complex environments, short foraging perches may not limit the area available that shrikes can search for prey to the degree that they would in a flatter environment. Two of the shrike territories we observed were in typically rocky canyons, and two were in shallower canyons flanked by flat mesas. Our results suggest that there may be an interaction between foraging-perch availability and topography, although our sample size was insufficient to demonstrate this conclusively.

With recent increases in the shrike population resulting from intensive population management—including the release of captive-bred shrikes into the wild—competition may play a greater role in the choice of defended foraging areas. To accommodate an increasing population, potential shrike habitat should be made available by the addition of hunting perches. Long-term improvement of shrike habitat should include restoring trees and shrubs to SCI to increase the availability of nesting habitat. Meanwhile, the lack of elevated hunting perches may be temporarily alleviated by the installation of artificial perches.

ACKNOWLEDGMENTS

Thanks to D. M. Cooper and K. M. Wakelee, who collected much of our data. Thanks to T. M. Ostheimer, W. A. Ostheimer, and the rest of the PRBO field crew who shared their observations and helped follow the shrikes. Thanks to P. Sharpe for reviewing our study design and to E. L. Kershner for encouraging the development of this manuscript and for insightful comments and suggestions. Thanks also to T. J. Cade, F. Chavez-Ramirez, and an anonymous reviewer for their critiques of this manuscript. This study was part of the recovery effort for the San Clemente Loggerhead Shrike and was funded by the Commander in Chief, Pacific Fleet, Pearl Harbor, Hawaii.

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The Wilson Journal of Ornithology 118(3):341–352, 2006

DO AMERICAN ROBINS ACQUIRE SONGS BY BOTH IMITATING AND INVENTING?

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ABSTRACT.—Although the majority of oscine species acquire a song repertoire by imitating songs they have been exposed to, some species also improvise and invent songs. To test the hypothesis that American Robins (*Turdus migratorius*) both imitate and invent the elements of their whistle songs, I analyzed the song repertoires of wild robins at three locations in western Massachusetts and the song development of five tutor-trained nestling robins. Robins appear to invent or improvise most of the elements in their repertoires (75–82%), but as fledglings and juveniles they acquire the remaining elements by imitating the songs of neighboring birds. *Received 29 April 2005, accepted 1 February 2006.*

Although it is generally agreed that birdsong serves two basic functions, mate attraction and territory maintenance (Catchpole and Slater 1995), there are striking differences in how various songbirds acquire the songs needed for these functions. In many species, young males imitate only conspecific songs heard during a sensitive period of song acquisition (Marler 1981, Catchpole and Slater 1995). In contrast, several species mimic heterospecific songs (e.g., Northern Mockingbird, *Mimus polyglottos*; Howard 1974, Owen-Ashley et al. 2002). Others not only mimic, but also create new versions of song through progressive modification of previously memorized song, known as improvisation, and/or through invention of entirely new songs unlike anything heard by the young bird (Marler and Peters 1982) (e.g., Gray Catbird, *Dumetella carolinensis*, Kroodsma et al. 1997). There are also species that rely almost entirely on improvisation or invention to develop songs (e.g., Sedge Wren, *Cistothorus platensis*, Kroodsma et al. 1999a). While imitation and mimicry are widespread among all taxa with vocal learning (e.g., dolphins, Tyack 1986; hummingbirds, Baptista and Schuchmann 1990; songbirds, Nelson et al. 1995; parrots, Hile et al. 2000), improvisation or invention has been documented in only a few songbird species (e.g., Nightingale, *Luscinia megarhynchos*, Hultsch and Kopp 1989; Indigo Bunting, *Passerina cyanea*, Payne 1996; Sedge Wren, Kroodsma et al. 1999a, Hughes et al. 2002) and possibly the signature whistles of dolphins (Sayigh 1990).

It is not understood why some species improvise or invent (Kroodsma 1996), nor is it known how extensive these tendencies are among songbirds or how many times they have evolved. A better understanding of the selective forces for improvising and inventing will emerge only after additional species are studied and only after life history traits are correlated to particular styles of song development. A challenge to such studies is that distinguishing between songs generated by improvisation, invention, or inaccurate imitation is difficult and often rather subjective. To distinguish improvisation from invention, the researcher must be able to document song elements changing over time, from something closely resembling tutor song to songs that may not resemble the tutor song at all. If, however, this period of improvisation is occurring during the winter months when a bird may be only mentally rehearsing song, it would be impossible to distinguish between these two types of song learning.

It has been suspected that American Robins (*Turdus migratorius*) improvise or invent when acquiring song. An early study of robin song found no shared song elements between any of the wild robins studied, even among neighbors (Konishi 1965). Konishi proposed two possible reasons for this lack of shared elements: (1) young robins improvise or invent the elements of their repertoires during the song acquisition phase, or (2) robins learn through imitation, but then disperse to breeding grounds where their song elements are unique (Konishi 1965). Later studies revealed

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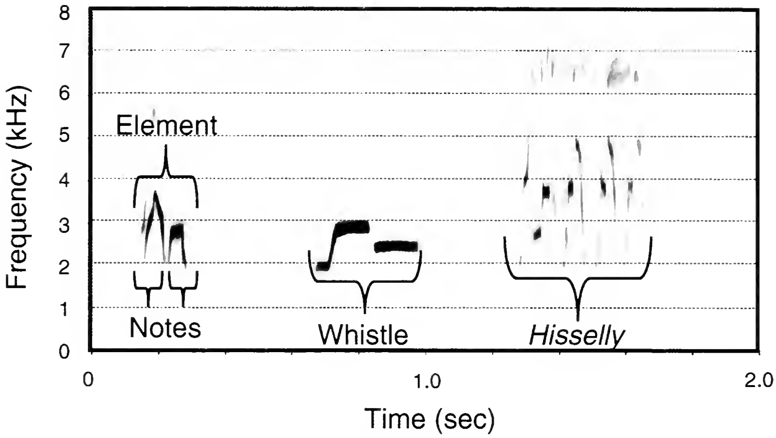

FIG. 1. A representative segment of American Robin song, recorded in western Massachusetts, 2002, showing the various structural units and their associated terms. Notes range from 25 to 250 msec in length and have a frequency range of 300 to 1,500 Hz. Elements range from 150 to 350 msec in length, and can have a frequency range of 1,000 to 7,000 Hz or wider. The time intervals between elements (250 to 2,000 msec) are always longer than the intervals between notes within an element (10 to 125 msec). Whistle elements have a narrow frequency range (mean frequency range = 1.78 ± 0.03 kHz, n = 46; Dziadosz 1977), with individual notes ranging from a low frequency of 1.5 kHz to a high of 4 kHz (Dziadosz 1977, Tsipoura 1985; SLJ pers. obs.). *Hisselly* elements have a wider frequency range (mean frequency range = 4.74 ± 0.24, n = 46 kHz, Dziadosz 1977) and more rapid frequency modulation (Konishi 1965). Some *hisselly* elements also show evidence of both syrinxes being used simultaneously, as found in other thrush species.

that robins shared one to five elements with neighboring robins (Dziadosz 1977, Thomas 1979, Tsipoura 1985, Sousa 1999), whereas most elements were unique (Tsipoura 1985). The fact that robins share a few elements with close neighbors but not with males from more distant locations (Dziadosz 1977, Sousa 1999) suggests that the shared elements are imitated, but that the unique elements are either improvised, invented, or learned elsewhere. Because of the difficulties in distinguishing between improvisation and invention, I refer to the song learning processes of robins in terms of imitation and invention, but with the understanding that robins may actually be improvising some song elements. Here I provide evidence that robins both imitate and invent/improvise song elements, based on research with both wild populations of robins and hand-reared nestlings.

METHODS

Description of robin song.—The song of the American Robin is composed of sequences of "song elements" that are made up of one or more "notes" shown as continuous markings on a spectrogram (Fig. 1). Male robins sing two song element types (Konishi 1965, Dziadosz 1977, Hsu 1991). The more common is the familiar whistle-like song usually described as some variation of *cheerily, cheer up, cheer up, cheerily, cheer up* (Sallabanks and James 1999). These elements generally sound like clear whistles, but can blend into buzzes or trills. Male robins typically have between 6 and 25 whistle elements in their repertoires (Sallabanks and James 1999; SLJ unpubl. data). The second type of element, described as the *hisselly,* or whisper, song (W. M. Tyler, as quoted in Bent 1949, and Young 1955, respectively), is generally sung very softly and has a much more complex structure. Robins tend to combine both whistle and *hisselly* elements to form groups typically consisting of 3–8 elements (Fig. 2). Although robins have a larger repertoire of *hisselly* than whistle elements, they typically sing whistle elements 5 to 10 times more frequently than *hisselly* elements (Konishi 1965; SLJ unpubl. data). Therefore, I chose to look for evidence of imitation and invention in the whistle elements of both wild and hand-reared robins.

Recording and analyzing songs of wild rob-

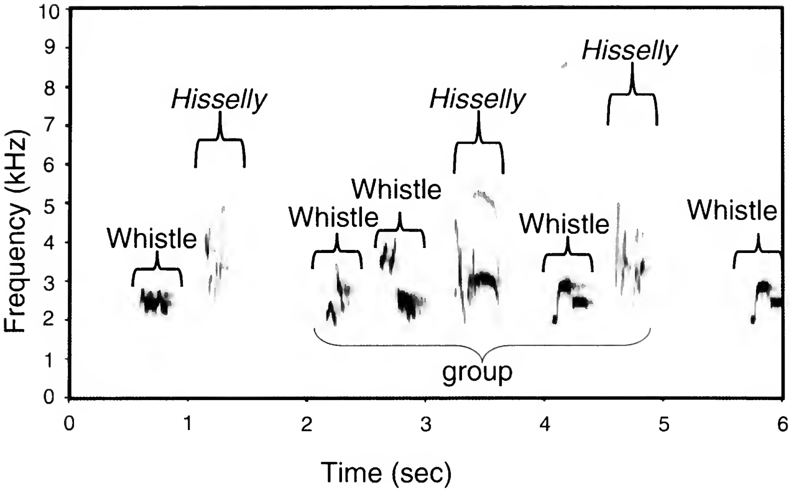

FIG. 2. Spectrogram showing the typical grouping of song elements by an American Robin in western Massachusetts. Robins combine both whistle and *hisselly* elements to form groups typically consisting of 3–8 elements.

ins.—I recorded the pre-dawn song of 42 male robins throughout the 2002 breeding season at three locations in Hampshire County, western Massachusetts: 16 birds at the Quabbin Cemetery (42° 16′ 48″ N, 72° 18′ 32″ W), 16 birds at Mt. Pollux Conservation Area (42° 19′ 39″ N, 72° 30′ 06″ W), and 11 birds at Wildwood Cemetery (42° 23′ 23″ N, 72° 30′ 44″ W). The three sites were between 6 and 21 km apart and consisted of open, mowed grassy areas with trees, shrubs, and wooded edges. From 18 April through 4 August 2002, I recorded twice per week at each of the three sites, beginning each day with the first robin song heard, generally 1–2 hr before sunrise, and ending at the first lull in singing after sunrise. Recording typically began at approximately 04:30 EST and ended before 07:00. Recordings were made with a Marantz PMD430 stereo cassette recorder and two Sennheiser ME62 microphones mounted on a Dan Gibson or a Telinga parabola. I attempted to record all the robins singing at each site each day and recorded two birds at a time whenever possible. I attempted to focus on any birds for which I had fewer recordings (i.e., less vocal individuals), and generally limited my recordings of the more vocal birds to 20 to 30 min each day.

I cataloged the song repertoires of individual birds by using field recordings made between 18 April and 16 May. During this period, I recorded 1 to 29 bouts per bird (mean = 8.5), with total recording time per bird ranging from 3 to 218 min (mean = 46 min). Because the robins were not banded and I conducted most recording when it was dark, I relied on the precise recording locations and the recordings themselves to determine individual repertoires. I began by noting the location of each bird as I recorded it, and then I determined the repertoire of song elements for each individual recording. I digitized the recordings (sample rate = 23,952.1 Hz) and then printed continuous spectrograms through Signal sound analysis software (Beeman 2003) with the settings as follows: transform length = 256 points, frequency resolution = 93.6 Hz, time resolution = 10.7 msec, and number of transformations = 2000. From the spectrogram of each recording, I determined the song element repertoire. The repertoires were very distinct, each being a unique combination of song elements primarily composed of elements found in no other repertoire. Another distinct feature of each repertoire was the order in which the elements were sung. During each recording of a specific repertoire, certain element combinations were sung much more than would be expected by chance; these combinations were very distinct and consistent over time. I also found that each repertoire of song elements was sung only in a small portion of the recording site. I recorded each repertoire repeatedly within a specific area, and these areas corresponded to approximate territories of robins observed after sunrise.

To verify that I had sufficient samples of each individual to allow me to determine complete repertoires, I randomly selected 200 sec of recording from each bird for which I had ample recordings, (and 180 sec from the one bird for which I had only 3 min of recording), and next plotted the number of different elements sung over time. In each case, element diversity reached an asymptote after 50 to 100 sec, suggesting that the complete repertoire was revealed. My results were similar to those of Konishi (1965), who found that American Robin repertoires were usually exhausted every 100 elements. During the robin's pre-dawn chorus, an individual will typically sing 100 elements in under 100 sec. The number of song elements revealed within each of the 200-sec samples was the same as the number of elements found for that individual throughout the total recordings made during the first half of the breeding season, and, in most cases, throughout the entire breeding season. Therefore, I feel confident that I had determined the complete repertoire of each bird sampled.

Next, I printed representative spectrograms (11 × 14 cm) of all song elements in each bird's repertoire from the best-quality recordings. Only a few of the elements showed any variability, and these were represented by multiple spectrograms. To assess repertoire overlap among males, five naïve observers were provided with a total of 315 spectrograms representing the song elements from all the recorded repertoires. Observers laid out all spectrograms and sorted the images by general similarities before searching for matching pairs of song elements, which generally took 8 to 10 hr. Identified pairs were then scored—rating their similarity on a six-level scale (0 to 5)—according to written instructions specifying the criteria for each level. A simplified version of the criteria follows: 0 = no similarity; 1 = elements have same general character, but <20% overlap; 2 = elements have some similarity, 20–49% overlap; 3 = elements are similar, 50–79% overlap; 4 = elements are very similar, 80–90% overlap; 5 = elements essentially the same, 91–100% overlap.

Because of the large number of potential comparisons, it was rare for all observers to identify a specific match; instead, typically two to four observers noted a given match. To ensure that the identified matches did represent very similar song elements, I and one of the original observers scored each match identified by one or more naïve observers, and rejected any matches that did not receive a score of 3 or higher from both of us.

To determine whether robins change their song elements or repertoires within the breeding season, I also evaluated repertoires in a second set of recordings made from 18 June through 4 August 2002. I compared the elements in the repertoires for each individual recorded during these later periods to the repertoires from the beginning of the 2002 breeding season.

Analyzing repertoire development in hand-reared robins.—In July 2002, I collected 14 nestling robins (4 to 14 days old) from six nests in Hampshire, Franklin, and Berkshire counties, Massachusetts. The nestlings were hand-reared in an animal care facility at the University of Massachusetts, Amherst, where they were fed a diet adapted from Lanyon (1979). Nest mates were initially raised together in the same cages. Soon after the young robins fledged, I placed each bird in its own cage and divided the birds into two groups of seven, separating siblings as much as possible and attempting to create similar sex ratios in the two groups. The apparent sex of each bird was based on the intensity of plumage color on the head and breast. Male robins generally have darker plumage in both of these regions. There were four apparent males in Group 1, and three males in Group 2. Because female American Robins also sing occasionally (Wauer 1999), I monitored all birds. Each group was housed in a separate isolation chamber (Acoustic Systems, Austin, Texas), and experienced daily periods of illumination mimicking the natural photoperiod.

Each group of robins was exposed to four tutor tapes, each containing the songs of a different wild robin. I created each tape from approximately 10 min of high-quality recording from one of four robins recorded in Amherst, Massachusetts. Each recording was repeated four to five times to fill one 45-min side of a cassette tape. The tapes were broadcast over two periods. The first tutor period began in August 2002, soon after the youngest birds fledged, at which time they ranged in age from 14 to 40 days; each group was exposed to two of the four tutor tapes during this period. On alternating days, tapes 1 and 2 were played in Chamber 1, and tapes 3 and 4 were played in Chamber 2. Tapes were played for the first 30 min of each daylight period and for 15 min at the end of the day. Each robin heard tutor song for 75 days during this first period.

The second tutor period began in early February 2003, at which time I switched the tapes between the two chambers, exposing the young birds to new song elements. The goal of exchanging the tapes was to evaluate whether the robins imitated sounds heard in their first spring as sub-adults. The young birds began singing on day 21 of this tutor period. I continued to play the tutor tapes for 5 more days and then began recording the young birds.

Using a preamplifier and two microphones, I recorded the young birds with a Nakamichi DR-3 cassette deck. To reduce the chances of recording birds other than the focal subject, I placed 5-cm acoustic foam around each microphone and cage, and, when recording quieter birds, I removed louder birds from the chamber. The young birds were recorded for two 30-min periods each day: the first 30 min of daylight and 30 min after feeding, when the birds often increased their rate of vocalization. I recorded the birds for 62 days from late February to early May.

Five of the birds identified as males produced song elements similar to those of wild robins; the remaining birds made only call notes. Four of the singing birds were in Group 1, and one was in Group 2. Two of the singing males in Group 1 were nest mates, while a third bird had a nest mate in Group 2. The song elements in each bird's repertoire remained stable throughout the 2.5-month recording period, and so appeared to represent crystallized song.

I digitized the recordings of the hand-reared birds and the tutor tapes, sampling at a rate of 20,000 Hz. I selected a representative example of each song element from each robin, and printed spectrograms using the same methods described above for the field recordings. Five naïve observers compared 331 representative spectrograms from the hand-reared and tutor repertoires. The same conditions and criteria for scoring similarity were followed as described above.

To determine whether the young robins had imitated adult song heard near their nest sites prior to capture, I compared each young bird's repertoire to that of adult robins (n = 3 to 6) from each nest site, as assessed from recordings made on the morning of capture or the day after. Representative spectrograms were printed and scored for similarity by two naïve observers, as described above. Means are presented ± SD.

RESULTS

Element similarity, repertoire delivery, and stability in wild robins.—Males from the same sites shared more song elements than those from different sites (Mann-Whitney test: $P < 0.001$, $n = 42$), suggesting that robins imitate some of the elements of local robins. The naïve observers identified 59 element pairs out of a possible 49,455 pairs, for which a majority of observers gave a similarity score of 3 or higher. Fifty-six of these identified pairs represented birds from the same recording site; their average similarity score was 3.7. The remaining three pairs represented elements recorded at different locations; no observer, however, gave a score higher than 3 for these pairs, and their average similarity score was 2.3. All matches found between multiple representatives of a single element type from within-bird repertoires were scored 4 or higher by the observers. Thirty-six of the 42 birds shared elements with other birds within their site. The percentage of elements in a bird's repertoire that were similar to elements in other repertoires at the same site ranged from 0 to 50% (mean = 25 ± 15% SD). In contrast, only five birds had elements that were judged as similar to elements of birds from different locations (Fig. 3). In each bird's repertoire, the percentage of elements that were similar to elements in the repertoires of birds from different sites ranged from 0 to 16.6%.

Most elements within each bird's repertoire were judged to be unique to that individual (mean = 75 ± 15% SD), indicating that the

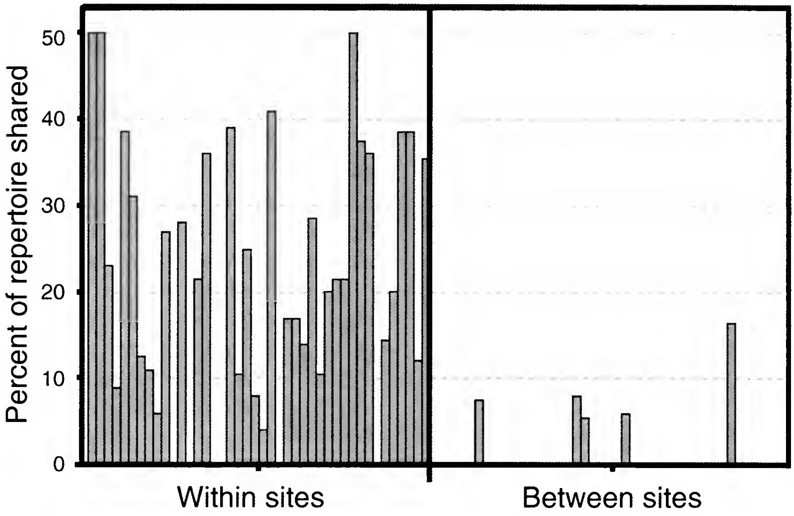

FIG. 3. Comparison of the percent of each American Robin repertoire shared within and between three sites in western Massachusetts, 2002. Each bar represents a single robin's repertoire. American Robins share far more elements with neighboring robins than with robins from different sites. The percent of shared elements in the repertoires of 42 robins is shown for both within and between sites. Note that 37 of 42 birds share 0% of their repertoire with birds from other sites.

robins either invented most of their song elements, learned them elsewhere, or learned them from a bird no longer present. In later recordings, these unique elements made it possible to identify each bird by its songs alone. The repertoires recorded during both the early and late periods retained the majority (mean = 98 ± 14%; *n* = 15 birds) of their elements throughout the entire season. However, the repertoires of six well-sampled birds (>440 sec of recording each period) did appear to change. One to two elements were added to two repertoires, and one to four elements were dropped from four repertoires. Two of these fluctuations may have been artifacts of unequal recording time between the two periods (i.e., the increase or decrease in repertoire size paralleled the increase or decrease in sample size between the two time periods), but the remaining four repertoire changes trend in the opposite direction from changes in the sample sizes between the two periods. For example, four of the elements in bird W3's early repertoire were missing in the later repertoire, despite an increase in recording time. Conversely, a new element was found in the late repertoire of Q3, despite a 97% reduction in recording time.

Some robins clearly modified individual elements over the course of the breeding season. Birds P6 and Q5 each sang one element that changed over the course of the breeding season (Fig. 4). In both cases, the new form completely replaced the old form. What was particularly striking about the change in Q5's case was that the later version was a much closer match to elements in three other repertoires from the same location (Fig. 5).

Song learning in hand-reared robins.—The tape-tutoring experiment provided evidence of both invention and imitation during song learning. The percentage of shared elements varied greatly among the five hand-reared robins that produced song. Two nest mates shared between 55.5 and 65% of their repertoires with each other, two other birds in this group, and the tutor tapes, whereas there were fewer shared elements in repertoires of the remaining three birds (range = 0–30%, mean = 14 ± 15% SD). There was almost no evidence of imitation of songs heard at the nest; one element of a single hand-reared bird was considered similar (average score 3) to an element recorded at that bird's nest site. These may have matched by chance, since both elements were simple descending whistles.

The remaining elements produced by the five birds did not match elements from the

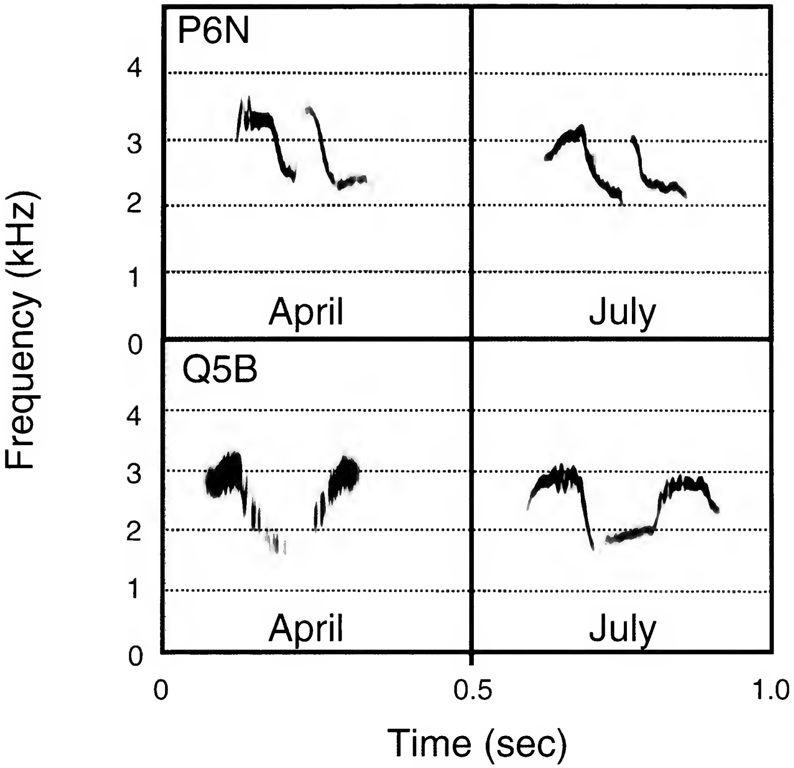

FIG. 4. Modifications of song elements over time from two wild American Robins (P6, element N; Q5, element B). Subjects were recorded in April and July 2002 in western Massachusetts.

nest sites, the tutor tapes, or other hand-reared birds, suggesting that the unique elements were either improvised or invented (Marler and Peters 1982, Nowicki et al. 2002). I compared examples of these elements at different times throughout the 62-day recording period and found no change over time, suggesting that the unique elements were invented, rather than improvised; however, I cannot eliminate the possibility that the young birds improvised changes during the winter silent period or before I began recording. I also compared the elements produced by the hand-reared birds to spectrograms of Konishi's (1965) isolated and deafened robins. I found that the elements produced by my hand-reared birds showed little or no within-element variability and consisted of whistle notes similar to those of wild

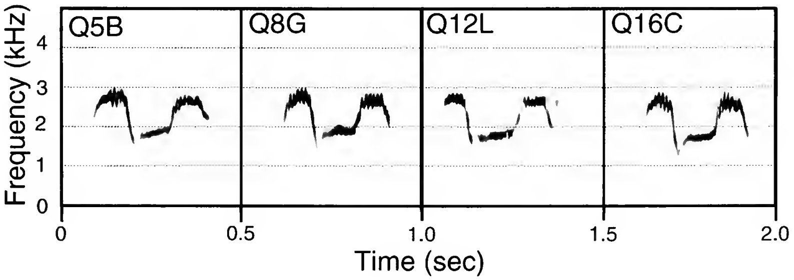

FIG. 5. Song elements of four American Robins recorded at the Quabbin Cemetery in Hampshire County, western Massachusetts, 2002. The late (July) version of bird Q5's element B is a closer match to elements in three local birds' repertoires than the early (April) version of bird Q5's element B in Figure 4.

TABLE 1. The number of song elements that four hand-reared birds (A2, F1, D1, and D2 in columns) within one isolation chamber shared among themselves and two tutor tapes (T1A and T1B). The highest incidence of sharing was between hand-reared siblings D1 and D2. F1 did not share any elements with two siblings raised in a separate chamber. All birds were reared and/or recorded in western Massachusetts, 2002.

Bird ID	A2	F1	D1	D2
T1A	1	1	0	0
T1B	0	1	0	0
A2	—	0	1	0
F1	0	—	3	2
D1	1	3	—	15
D2	0	2	15	—

robins, whereas Konishi's birds produced songs with a high degree of within-element variability; elements consisted of wavering whistle notes. This suggests that the song elements produced by the hand-reared birds were fully crystallized, invented/improvised songs, rather than the basic acoustic features of song that can be produced by isolated birds.

Although most of the elements were invented/improvised, imitation was also evident in four of the young birds' repertoires. The young birds tended to share more elements with other hand-reared birds than with the tutor tapes (Table 1). The naïve observers identified 24 pairs of elements, the average similarity scores of which were ≥3, indicating a high degree of similarity. Fifteen of the 24 identified pairs were between two siblings housed in the same chamber (see Fig. 6 for examples). Two of the elements shared by these siblings were also sung by non-siblings housed within the same chamber. Six pairs were between non-siblings within the same chamber, and three pairs were between tutors and young birds (see Fig. 7 for example). The imitated tutor elements were from tapes played only during the first tutoring period, whereas the elements shared between birds could not have been heard until the birds were old enough to sing. No elements were shared between the birds in Group 1 and the single singing bird in Group 2, even though this bird had two male siblings in Group 1.

The percentage of shared elements in each bird's repertoire varied greatly. Bird A2 shared 30% of its repertoire, Bird D1 65%, Bird D2 55.5%, Bird F1 13%, and Bird F2 0% (mean = 32.8 ± 27.5% SD). The degree of sharing in A2, F1, and F2 falls within the range of sharing I found for wild robins; however, that of the siblings D1 and D2 was much greater due to the percentage of elements they shared with each other (63% and 42%, respectively).

DISCUSSION

The field recording and tape-tutoring components of this study indicate that American Robins can and do imitate song elements. Among repertoires of wild robins, closely matching song elements were found within sites, but only weak similarities were found between sites, indicating that the matching elements were imitated. Additional evidence of imitation was found in the case of one bird at the Quabbin site that changed one element to more closely match an element shared by three other birds from that site, indicating that robins can change their repertoires to match other birds. Because the ages of the recorded robins were not known, it has yet to be determined whether this ability is restricted to the first breeding season.

A similar pattern was found in the repertoires of hand-reared birds, which together produced three close matches to elements from tutor tapes. In addition, birds kept within a single chamber produced 21 closely matching elements, but there were no matching elements between birds raised in separate chambers. The fact that the 21 matching elements between birds could not have been learned until the birds began singing also supports the idea that adult robins—at least in their first breeding season—can change, or add to, their repertoires. Closely related Blackbirds (*Turdus merula*) also appear to continue learning songs as adults (Rasmussen and Dabelsteen 2002). A possible limitation on the interpretation of these results is that tutor tapes, rather than live tutors, were used, and the stimulus of live tutors, as experienced in nature, may elicit a higher degree of imitation.

Robins may have a tendency to learn song elements that are heard more often, either because they are sung by multiple birds, or are sung by a highly vocal bird. My data offer some support for this tendency. Two of the

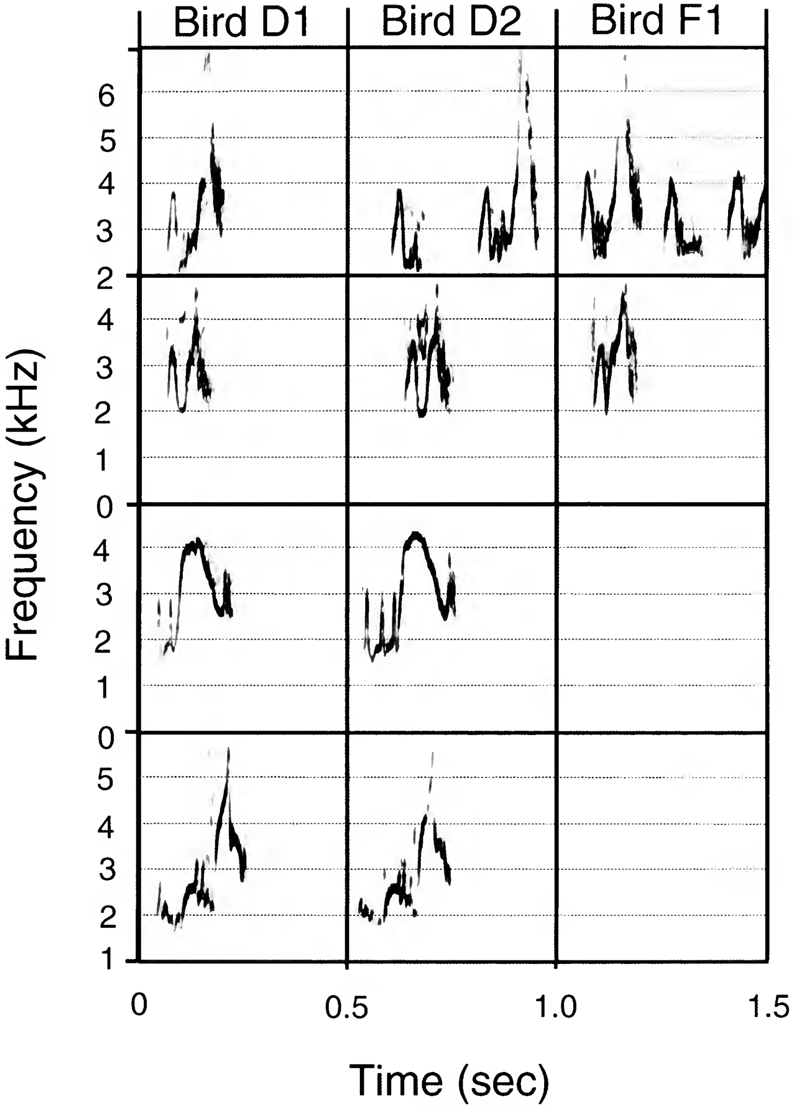

FIG. 6. Four examples of song element sharing between three hand-reared American Robins raised in one chamber in western Massachusetts, 2002. Birds D1 and D2 are brothers and shared more elements than any other hand-reared birds. The lower two elements were shared only by D1 and D2, not by F1.

song elements sung by the hand-reared robins were shared by three individuals, and many of the elements shared by wild robins were shared by three or more individuals. It also appears that one wild robin altered one element in his repertoire to more closely match that of three other robins within his particular recording area.

Robins also appear to invent or improvise song elements. The majority of elements produced by the tape-tutored birds were unique for each individual, indicating that the elements were invented/improvised by the tutored birds. The majority of elements in the wild robin repertoires were also unique to each individual, which suggests that invention or improvisation also could be involved in song acquisition in the wild. However, I cannot rule out the possibility that at least some of these elements may have been learned elsewhere or from birds no longer present at the local site.

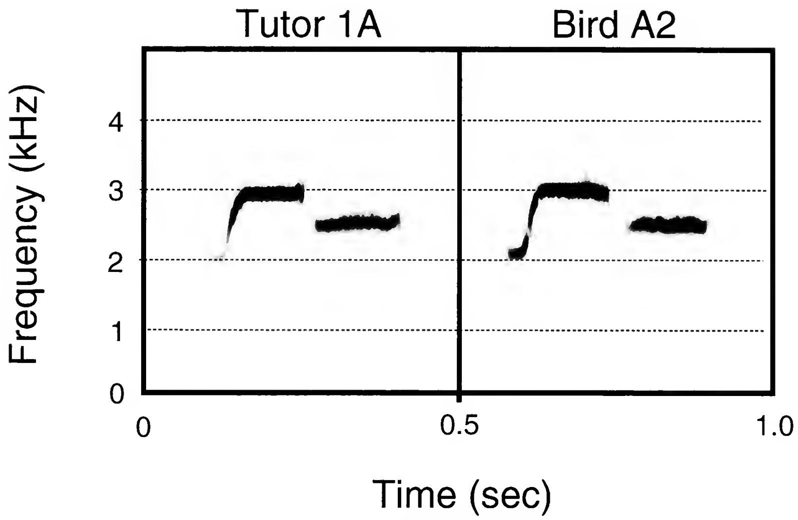

FIG. 7. Example of song element matching between tutor tape 1A and hand-reared American Robin A2, western Massachusetts, 2002.

My results are not completely consistent with either of Konishi's (1965) hypotheses on robin song development. Konishi found no evidence of element matching, and he explained this by suggesting that either robins improvise/invent the elements of their repertoires during song acquisition, or they learn through imitation and then disperse to breeding grounds where their song elements are unique (Konishi 1965). My results suggest that robins do improvise/invent songs, but also imitate songs of nearby robins, and that these imitations occur during both early song acquisition and after robins settle on breeding territories, allowing adult birds to share song elements with local males.

Song sharing plays an important role in the communication of several species. For example, neighboring males in many species song-match during territory defense as a warning of potential escalation (Krebs et al. 1981, Falls et al. 1982, Beecher et al. 2000a). A benefit of this system is illustrated in Song Sparrows by the positive correlation between how long a male holds a territory and his ability to share songs with his neighbors (Beecher et al. 2000b). Robins also may benefit from sharing elements in their repertoire; although they may not song-match, most robins sing the shared elements in their repertoire more than would be expected by chance (SLJ unpubl. data). It is also worth noting that only three robins recorded during the first third of the breeding season did not share elements with other birds at their sites, and that none of these birds could be found in the last third of the season.

The results of my tape-tutoring experiment indicated that social interaction with live birds provided stronger stimulation for imitation than tutor tapes—as found in many studies (e.g., Beecher 1996), suggesting that the benefit of sharing elements is tied to social interactions. A particularly interesting result of this experiment is the high percentage of element sharing between the two siblings with visual and acoustical access to each other. This contrasts with the lower percentage of sharing with other, equally accessible birds in the same chamber, and with the complete lack of sharing between the siblings raised in different chambers. It appears unlikely that this high degree of sharing is a result of songs learned and imitated from parents or neighbors during the nestling period. One possible interpretation is that there is a predisposition to learn from one's relatives (Nelson and Marler 2005). Further research into the social interactions between adult and fledgling robins, particularly between closely related birds, may provide additional clues to the importance of shared elements in American Robins.

Why American Robins both imitate and invent during song development remains a mystery. A key to unraveling this mystery is the fact that song development evolves in response to selection pressures brought about by other life-history traits (Kroodsma 1983). For example, some highly migratory or nomadic species tend to improvise or invent a higher percentage of their songs than closely related species and subspecies that are non-migratory and/or exhibit greater philopatry (Kroodsma et al. 1999a, b; Nelson et al. 2001; Handley and Nelson 2005). We can address the question of why a species invents and/or imitates by looking for correlations between song development and life-history traits (e.g., migratory status, philopatry) among closely related groups (e.g., Read and Weary 1992, Nelson et al. 1995). The American Robin, with seven subspecies, including one that is non-migratory, promises to be an excellent subject for such a comparative study. With 65 congeners (Phillips 1991), the robin could also be part of a much broader study that incorporates a wide range of traits in song development and life history.

ACKNOWLEDGMENTS

I thank D. E. Kroodsma and B. E. Byers for their invaluable advice and Jeff Podos for providing the acoustic isolation chambers and room for raising young robins. I also wish to thank L. Johnson, S. Huber, K. Belinsky, J. Southall, C. Kennedy, M. Miller, and J. Claude Razafimahaimodison for their long hours searching for element matches. This project was funded in part by a GAANN Fellowship Grant. The Massachusetts Department of Fish and Wildlife and the U.S. Fish and Wildlife Service provided scientific collecting permits. I also wish to thank three anonymous reviewers for their comments and suggestions.

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The Wilson Journal of Ornithology 118(3):353–363, 2006

EFFECTS OF MOWING AND BURNING ON SHRUBLAND AND GRASSLAND BIRDS ON NANTUCKET ISLAND, MASSACHUSETTS

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ABSTRACT.—Throughout the United States, declines in breeding populations of grassland and shrubland birds have prompted conservation agencies and organizations to manage and restore early-successional habitats. These habitats support a variety of birds, some of which have been classified as generalists; thus, often these birds are thought to be less affected by habitat manipulation. More information, however, is needed on the response of early-successional generalists to habitat management, because conservation agencies are increasing their focus on the regional preservation and management of common species. On Nantucket Island, Massachusetts, the goal of the Partnership for Harrier Habitat Preservation (PHHP) has been to restore more than 373 ha of grassland for the island's population of Northern Harriers (*Circus cyaneus*). This management program has entailed methods such as prescribed burning and mowing (e.g., brushcutting) to restore and maintain grassland habitat. Over a 3-year period, we found that songbird response to burning and mowing varied among species, depending on subtle habitat preferences and the intensity and type of management. In shrublands, Eastern Towhee (*Pipilo erythrophthalmus*) and Common Yellowthroat (*Geothlypis trichas*) abundance declined in mowed areas but were unaffected by prescribed burning. In grasslands, Savannah Sparrow (*Passerculus sandwichensis*) abundance showed no response to either burning or mowing, whereas Song Sparrows (*Melospiza melodia*) preferred unmanaged grasslands. In shrublands, mowing was the most effective method for restoring grassland habitat, whereas prescribed burning had little effect on abundances of shrubland birds and vegetation structure. In grasslands, both mowing and burning were successful in restricting shrubland encroachment and maintaining grassland habitat. *Received 27 June 2005, accepted 1 March 2006.*

Between 1966 and 2004, there have been significant population declines in 10 of 14 (71%) grassland and 16 of 36 (44%) shrubland bird species within the eastern Breeding Bird Survey region (Sauer et al. 2005)—a result of habitat loss and fragmentation (Vickery 1992, Askins 2002, Confer and Pascoe 2003, Dettmers 2003, Vickery et al. 2005). Because of these population declines, prescribed burning and mowing have become increasingly important conservation tools in managing grasslands and shrublands throughout the northeastern United States (Vickery et al. 2005).

Efforts to restore and maintain early-successional areas traditionally focused on providing habitat for rare and threatened grassland specialists. Consequently, researchers often emphasize the effects of habitat disturbance on single species that tend to be habitat specialists (i.e., species with rigid habitat requirements) rather than habitat generalists (i.e., species with broad habitat requirements; Bayne and Hobson 2001, Fort and Otter 2004). As regional programs, such as Partners in Flight (Rich et al. 2004) and the National Gap Analysis Program (Scott et al. 1993), continue to advocate a conservation approach of "keeping common species common," there is a greater need to study the effects of habitat disturbance and management on generalist species. Although studies have addressed the effects of rangeland management on early-successional songbirds in the western United States (e.g., Wiens and Rotenberry 1985, Wiens et al. 1986) and the effects of management on grassland birds in northeastern and midwestern sectors of the country (Bollinger et al. 1990, Herkert et al. 1999, Johnson et al. 2004), no studies have focused on the effects of large-scale grassland restoration on both grassland and shrubland generalists in the northeastern United States.

Massachusetts' coastal sandplain grasslands, heathlands, and shrublands are important regional conservation priorities because they support unique regional biodiversity

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(Barbour et al. 1999). It is estimated that more than 90% of coastal heathlands and grasslands in the northeastern United States have been lost since the middle of the 19th century due to development, cultivation, and shrubland encroachment (Barbour et al. 1999). The largest remaining contiguous areas of sandplain grasslands and coastal heathlands in the Northeast are found on Nantucket Island (hereafter Nantucket; Tiffney and Eveleigh 1985, Dunwiddie 1989). Currently, Nantucket's grasslands and heathlands are being lost to increasing residential development and shrubland encroachment (Tiffney and Eveleigh 1985, Dunwiddie and Caljouw 1990, Barbour et al. 1999), the latter representing an important cause of both habitat loss and degradation for grassland birds.

Many of Nantucket's shrubland and grassland areas have been targeted for restoration and management. In 1996, the Partnership for Harrier Habitat Preservation (PHHP) was formed to develop a large-scale vegetation management program aimed at restoring >373 ha of grassland to create and sustain habitat for Northern Harriers (*Circus cyaneus*), an obligate grassland species that requires relatively open areas for most of its breeding cycle (Christiansen and Reinert 1990, Dechant et al. 2003). This program has entailed two basic methods of restoration and management: prescribed burning and mechanical restoration (i.e., brush cutting and repeated mowing; Combs-Beattie and Steinauer 2001). Although the goals of the PHHP emphasize the creation of habitat for Northern Harriers, Nantucket's shrublands and grasslands support several regionally declining generalist species whose habitat preferences are relatively broad, including Eastern Towhees (*Pipilo erythrophthalmus*; Greenlaw 1996), Savannah Sparrows (*Passerculus sandwichensis*; Wheelwright and Rising 1993), Common Yellowthroats (*Geothlypis trichas*; Guzy and Ritchison 1999), and Song Sparrows (*Melospiza melodia*; Arcese et al. 2002).

Our goal was to document the effects of prescribed burning and mowing on Nantucket's assemblage of shrubland and grassland songbirds. In so doing, our objectives were to (1) document changes in vegetation structure in response to management, (2) identify habitat associations of shrubland and grassland songbirds, and (3) analyze the response of shrubland and grassland generalists to habitat alteration. Habitat restoration can be a powerful conservation tool, but considering the regional goals and objectives of many conservation programs aimed at preserving common species, we believe that it is important to study the effects of habitat management on habitat generalists, as well as specialists.

METHODS

Study areas.—Nantucket (41° 28.3′ N, 70° 1′ W) is about 48 km south of Cape Cod and measures 11 × 24 km (Litchfield 1994). The island contains naturally occurring and regionally rare sandplain grasslands, scrub oak shrublands, and sandplain heathlands (Swain and Kearsley 2001). The sandplain grasslands are dominated by graminoids, primarily little bluestem (*Schizachyrium scoparium*), Pennsylvania sedge (*Carex pensylvanica*), and poverty oatgrass (*Danthonia spicata*). Scrub oak shrublands are dominated by bear oak (*Quercus ilicifolia*) and have an understory of black huckleberry (*Gaylussacia baccata*), bearberry (*Arctostaphylos uva-ursi*), and lowbush blueberry (*Vaccinium angustifolium*; Dunwiddie and Sorrie 1996). Heathlands support many of the same plant species as those found in grasslands and scrub oak shrublands, but are dominated by low-growing black huckleberry, bearberry, and lowbush blueberry (Swain and Kearsley 2001). Despite sharing many of the same characteristic plant species as shrublands, heathlands found along the coastline are noticeably shorter and often intermix and overlap with grassland communities; consequently, we defined grassland/heathland areas as grassland for subsequent analyses (Dunwiddie and Sorrie 1996).

From 1998 to 2001, the PHHP targeted >373 ha of shrubland and grassland for restoration and maintenance (Table 1). Management plans have included prescribed burning on 142 ha of scrub oak shrubland and >26 ha of grassland/heathland, and repeated mowing and brush cutting on 205 ha of shrubland (Table 1). The frequency of management differed among study sites: shrubland areas were burned no more than once, and mowing frequency ranged from 0 (control areas) to 1–3 cuts annually. In addition to these activities, the Nantucket Land Bank Commission began

TABLE 1. Management areas and restoration histories of grassland and shrubland study sites on Nantucket Island, Massachusetts, 1999–2001.

Site name	Area (ha)	No. bird survey plots	Restoration history	Years sampled
Shrublands				
D	19.4	6	Control/burn (2000)	1999–2001
E1	19.3	8	Control	1999–2001
SHRUB	14.2	5	Control	1999–2001
BC	68.0	12	Mow (1998–2001)	1999–2001
A	10.5	4	Mow (1998, 1999)	1999
LB1	19.8	5	Mow (1999–2001)	2000–2001
LB2	19.0	5	Mow (1999–2001)	2000–2001
A2	9.7	3	Mow (2000)	2000–2001
TRI	6.9	3	Mow (2000, 2001)	2000–2001
LB4	21.0	8	Mow (1999–2001)	2001
ABURN	10.9	4	Burn (2000)	2001
E2	16.2	4	Burn (1994)	1999–2001
E3	0.8	1	Burn (1998)	1999–2001
F	4.9	3	Burn (1996)	1999–2001
Grasslands				
LRAM	4.5	3	Control/burn (2001)	1999–2001
HPLAIN	19.0	6	Control	1999–2001
LB3	12.1	5	Control	2000–2001
RAM	30.8	6	Mow (1999, 2000)/burn (2001)	1999–2001
GOLF	6.1	4	Mow (1998–2001)	1999–2001
AIR	7.7	4	Mow (1998–2001)	1999–2001

similar brush-cutting efforts in three separate areas comprising >74 ha. Study sites consisted of areas that were either controls (grasslands, shrublands, or heathlands that had not been managed for at least 10 years) or areas that had received or are receiving management through mowing or prescribed burning since 1988. Given the duration of the management plan, the number of areas being managed and surveyed changed each year (Table 1). Management areas were typically discrete subsets of larger, more contiguous habitats that were receiving a particular treatment. No two adjacent study areas shared the same treatment history, and study areas were spatially separated by other habitat types or barriers (e.g., wetlands, open water, or roads). To avoid disruption due to treatment activities, we collected data only in those areas that were not being actively managed during the summer months of this study. Due to unexpected summer management activities on some study sites, we did not sample every site in each year; thus, the number of observations differed among study sites and sample data were unbalanced (Table 1).

Bird censuses.—In the breeding seasons of 1999–2001, we determined avian abundance of shrubland and grassland songbirds by conducting 10-min avian surveys in fixed-radius, 50-m circular plots along pre-established parallel transects, the length and number of which varied, depending on the size and configuration of each site (Table 1; Bibby et al. 2000). Survey plots were >100 m from any habitat edges and >200 m from other plots (Hutto et al. 1986, Bibby et al. 2000). From 22 May to 10 August during the breeding seasons of 1999–2001, we visited 14 shrubland and 6 grassland sites three times (Vickery et al. 1994). We conducted surveys between 06:00 and 10:00 EDT and began surveys 2 min after arriving at the site, but we did not survey birds during inclement weather, such as rain or high wind (>15 km/hr; Vickery et al. 1994). Because our focus was limited to avian and vegetation changes only within management areas, our protocol purposely did not account for changes along or near habitat edges. For a given breeding season, we considered the maximum number of singing males detected during our three visits as a measure of avian abundance, and combined these data to derive a mean for all survey plots within a particular management area.

Vegetation surveys.—At each survey plot, we sampled the vegetation at 0.5-m intervals along four 50-m transects that radiated from the center of each survey plot in the four cardinal directions (Brower and Zar 1977). This resulted in 400 vegetation sampling points per survey plot. At each sampling point, we recorded the dominant vegetation type and height. We classified vegetation cover into four type categories (sparse vegetation, litter, grass/forb, and shrub) and seven height categories (0, >0–0.1, >0.1–0.5, >0.5–1.0, >1.0–2.0, >2.0–5.0, and >5.0 m. Vegetation data were converted to relative frequencies and, for a given parameter in a given survey plot, we averaged all values from the four transects. This method allowed us to establish a basic portrait of vegetation height and type for each point count and study site.

Statistical analyses.—Our null hypothesis was that that bird densities within control shrublands and grasslands would be the same as those in managed shrublands and grasslands, respectively. We used univariate methods to determine species-specific responses to restoration techniques and vegetation characteristics. We were unable to randomize our treatments because management of this large, multi-agency restoration program was constrained by multiple factors beyond our control. This is not uncommon in "natural experiments" and we employed matching in lieu of a controlled experimental design; that is, we compared managed units with units that were not managed (i.e., control), but were similar to the treated units in terms of proximity and environmental conditions (Johnson 2002).

We used a proportional odds logistic regression model with forward selection to identify significant vegetation predictors of avian occurrence (Hosmer and Lemeshow 1989; PROC LOGISTIC; SAS Institute, Inc. 1990). Heavily skewed data on vegetation and uncommon bird species that did not satisfy normality requirements were converted to detection/non-detection (i.e., presence/absence) data for further analysis. For these data, we used chi-square analysis to determine which vegetation variables influenced the detection/non-detection (i.e., presense/absence) of selected bird species (Kleinbaum et al. 1998); only vegetation variables that were significant ($\alpha < 0.05$) in this analysis were used in the logistic regression models (Hosmer and Lemeshow 1989).

We used repeated-measures analysis of variance (ANOVA) to determine bird species-specific responses to management (Sokal and Rohlf 1995). Due to the unbalanced nature of the study design, we used SAS (PROC MIXED; SAS Institute, Inc. 1990), which allows for interval-independent variables and uses the maximum likelihood method to estimate parameters (Kleinbaum et al. 1998). Study sites that received the prescribed burning treatment were categorized by two post-burn classifications: 1 year post-burn and 2–7 years post-burn. One-way ANOVAs were used to determine differences in vegetation variables within grasslands and shrublands treated with different methods and, because all pairwise comparisons were of interest, we used the Tukey-Kramer method for all multiple-comparison tests (Kleinbaum et al. 1998). We conducted ANOVAs separately on grassland/heathland and shrubland areas for both bird abundance and vegetation data. The densities of three species—Eastern Towhee, Savannah Sparrow, and Song Sparrow—were adequate to meet the requirements for repeated measures ANOVA. We set (*a priori*) a significance level of $P = 0.05$ and a "marginal" significance level of $0.10 > P > 0.05$. We conducted power analyses on ANOVA results at a significance level of $P = 0.05$. Means are presented ± SE.

RESULTS

Changes in vegetation structure.—Mowing and burning had different effects on vegetation structure and composition (Table 2). Mowing in shrublands produced the most notable difference. Mowed shrublands had a greater percent cover of litter (37.7% ± 17.5) than burned (2.3% ± 2.1) or control areas (1.9% ± 1.8; $F_{2,12} = 15.22$, $P < 0.001$). Medium-height shrubs (1.0–2.0 m) were common in control (44.4% ± 12.1) and burned shrublands (47.3% ± 14.5) but significantly less in mowed shrublands (11.1% ± 8.3; $F_{2,12} = 17.82$, $P < 0.001$). We documented similar findings for tall shrubs (2.0–5.0 m; $F_{2,12} = 9.17$, $P = 0.004$). Although not significant at the 0.05 alpha level, medium-height grasses

TABLE 2. Percent cover (SE) for vegetation variables, and results of one-way analysis of variance (ANOVA), testing treatment effects in shrubland and grassland habitats on Nantucket Island, Massachusetts, 1999–2001. Several vegetation variables changed in response to mowing and prescribed burning in shrubland and grassland study sites. In shrubland sites, mowed areas had greater proportions of litter and short shrubs and lower proportions of medium and tall shrubs. In grassland sites, unmanaged grasslands had higher proportions of medium shrubs. Significant values ($P < 0.05$) are in bold.

Variable entered	Control	Burn	Mow	*P*
Shrublands				
Sparse vegetation	0.04 (0.04)	0.08 (0.04)	0.03 (0.04)	0.091
Litter (0–0.1 m)	0.02 (0.02)	0.02 (0.02)	0.38 (0.17)	**<0.001**
Short grass (0–0.1 m)	0.01 (0.02)	0.00 (0.01)	0.07 (0.07)	0.10
Medium-height grass (0.1–0.5 m)	0.16 (0.03)	0.11 (0.11)	0.28 (0.13)	0.079
Short shrub (0–0.1 m)	0.50 (0.19)	0.34 (0.32)	0.24 (0.22)	0.36
Short shrub (0.1–0.5 m)	0.46 (0.06)	0.50 (0.10)	0.72 (0.14)	**0.006**
Medium-height shrub (0.5–1.0 m)	0.39 (0.11)	0.33 (0.10)	0.37 (0.14)	0.82
Medium-height shrub (1.0–2.0 m)	0.44 (0.12)	0.47 (0.15)	0.11 (0.08)	**<0.001**
Tall shrub (2.0–5.0 m)	0.44 (0.09)	0.46 (0.17)	0.15 (0.13)	**0.004**
Tall shrub (>5.0 m)	0.04 (0.04)	0.07 (0.11)	0.06 (0.06)	0.88
Grasslands				
Short grass (0–0.1 m)	0.13 (0.12)	0.30 (0.00)	0.53 (0.17)	**0.046**
Medium-height grass (0.1–0.5 m)	0.66 (0.11)	0.75 (0.01)	0.65 (0.07)	0.43
Short shrub (0–0.1 m)	0.26 (0.02)	0.37 (0.10)	0.32 (0.25)	0.73
Short shrub (0.1–0.5 m)	0.67 (0.10)	0.55 (0.02)	0.39 (0.19)	0.13
Medium-height shrub (0.5–1.0 m)	0.38 (0.07)	0.14 (0.10)	0.13 (0.04)	**0.025**
Medium-height shrub (1.0–2.0 m)	0.08 (0.00)	0.00 (0.00)	0.03 (0.01)	0.67
Tall shrub (2.0–5.0 m)	0.01 (0.03)	0.00 (0.00)	0.04 (0.07)	0.67

(0.1–0.5 m), which were uncommon in control (15.6% ± 3.3) and burned (11.3% ± 11.2) shrublands, were slightly more common in mowed areas (27.7% ± 13.1; $F_{2,12} = 3.14$, $P = 0.080$).

In grasslands, burning and mowing produced notable differences in vegetation (Table 2). Compared with grasslands that had been burned or mowed, control grasslands were characterized by a relatively greater percent cover of short-shrub vegetation. Medium-height shrubs (0.5–1.0 m) were more abundant in control grasslands (37.6% ± 6.7), and less abundant in burned (13.7% ± 10.1) or mowed grasslands (12.7% ± 4.4; $F_{2,4} = 8.37$, $P = 0.025$). Mowed grasslands had higher proportions of short grass (0.0–0.1 m; 52.6% ± 17.0) compared with burned (30.0 ± 0.0%) and control grasslands (13.0% ± 12.0; $F_{2,4} = 6.08$, $P = 0.046$).

Avian response to vegetation.—Shrubland and grassland bird communities on Nantucket were relatively depauperate, a common characteristic of faunal communities on islands (Brown and Lomolino 1998). Important vegetation predictors of Eastern Towhee, Common Yellowthroat, Song Sparrow, and Savannah Sparrow presence varied by species (Table 3). Towhees were positively associated with litter (0–0.1 m) and medium (1.0–2.0 m) and tall (2.0–5.0 m) shrubs, but they were negatively associated with medium-height grass (0.1–0.5 m; Table 3). Unlike towhees, Common Yellowthroats were negatively associated with litter (0–0.1 m) but positively associated with medium shrubs (1.0–2.0 m). Song Sparrows were positively associated with medium-height grass (0.1–0.5 m) and medium shrubs (0.5–1.0 m), but they were negatively associated with litter (0–0.1 m). Savannah Sparrows were positively associated with medium grass (0.1–0.5 m) but negatively associated with litter (0–0.1 m) and tall shrubs (2.0–5.0 m; Table 3).

Avian response to management within shrublands.—Within shrubland areas, we recorded Eastern Towhees, Common Yellowthroats, Song Sparrows, Gray Catbirds (*Dumetella carolinensis*), Eastern Kingbirds (*Tyrannus tyrannus*), Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), and Prairie Warblers (*Dendroica*

TABLE 3. Proportional odds logistic regression using percent cover of vegetation predictors to model the probability of bird species presence in shrubland and grassland habitat on Nantucket Island, Massachusetts, 1999–2001. Significant values ($P < 0.05$) are in bold.

Variable entered	Estimate	Standard error	*P*
Eastern Towhee			
Bare ground	−0.57	0.40	0.15
Litter (0–0.1 m)	1.35	0.41	**0.001**
Short grass (0–0.1 m)	0.26	0.49	0.60
Medium-height grass (0.1–0.5 m)	−0.85	0.43	**0.05**
Tall grass (0.5–1.0 m)	−1.55	1.07	0.15
Medium-height shrub (0.5–1.0 m)	−0.10	0.69	0.88
Medium-height shrub (1.0–2.0 m)	1.20	0.50	**<0.001**
Tall shrub (2.0–5.0 m)	1.67	0.39	**<0.001**
Tall shrub (>5.0 m)	0.31	0.78	0.69
Common Yellowthroat			
Litter (0–0.1 m)	−0.88	0.38	**0.02**
Short grass (0–0.1 m)	−0.34	0.61	0.57
Medium-height grass (0.1–0.5 m)	−0.26	0.42	0.54
Medium-height shrub (1.0–2.0 m)	1.18	0.62	**0.05**
Tall shrub (2.0–5.0 m)	0.64	0.48	0.18
Song Sparrow			
Litter (0–0.1 m)	−1.09	0.37	**0.004**
Medium-height grass (0.1–0.5 m)	1.97	0.50	**<0.001**
Medium-height shrub (0.5–1.0 m)	1.63	0.54	**0.003**
Tall shrub (>5.0 m)	−1.03	0.83	0.22
Savannah Sparrow			
Litter (0–0.1 m)	−2.85	0.74	**<0.001**
Short grass (0–0.1 m)	0.14	0.45	0.80
Medium-height grass (0.1–0.5 m)	2.13	0.89	**0.02**
Short shrub (0–0.1 m)	−0.26	0.61	0.68
Medium-height shrub (0.5–1.0 m)	−0.32	0.46	0.49
Medium-height shrub (1.0–2.0 m)	−0.53	0.48	0.26
Tall shrub (2.0–5.0 m)	−2.78	0.75	**<0.001**

discolor). Eastern Towhees showed a clear response to management practices in shrublands (Table 4). In two out of the three breeding seasons, Eastern Towhee abundance was greater in control or burned shrublands compared with shrublands that had been mowed. Overall, towhee abundance was greatest in areas that had been burned (1.42/ha ± 0.49), and there was no difference in densities between controls (1.12/ha ± 0.37) and mowed areas (0.66/ha ± 0.50; Fig. 1); however, our power to detect this difference was low ($\beta = 0.09$). The abundance of towhees differed significantly among years (Table 4), decreasing in every season from an average of 1.48 ± 0.86 in 1999 to 0.86 ± 0.75 in 2000 to 0.71 ± 0.64 in 2001.

Towhee abundance decreased as the frequency of mowing increased between sites (Table 4). After a single mowing event, towhee abundance dropped from an average of 1.13/ha ± 0.17 to 0.85/ha ± 0.17. After a second mowing, abundance further declined to 0.53/ha ± 0.18, although this decrease was not significant; again, however, our power to detect significant differences was limited ($\beta = 0.3$).

We found no significant differences in towhee abundance in relation to time since the most recent burn (Table 4), but power was low ($\beta = 0.21$). Although towhee abundance declined slightly in the first year after a burn, this decline was not significant, and abundance in sites that had been burned 2–7 years earlier was not significantly different than the abundance in control areas.

Among the less common shrubland birds, Common Yellowthroats preferred control and

TABLE 4. Repeated measures analysis of variance (ANOVA) testing treatment effects on Eastern Towhees in shrubland habitats on Nantucket Island, Massachusetts, 1999–2001. Densities of Eastern Towhees were most affected by mowing and the frequency of mowing within shrubland sites; prescribed burning had little effect on Eastern Towhee abundance. Significant values ($P < 0.05$) are in bold.

Variable entered[a]	df	Estimate	Standard error	F or t	P
Treatment comparisons	2, 12			4.25	**0.040**
Control versus burn	12	0.30	0.31	0.94	0.63
Burn versus mow	12	−0.76	0.29	2.84	**0.037**
Control versus mow	12	−0.47	0.28	1.64	0.27
Mowing frequency	2, 4			5.25	**0.035**
Control versus 1 mowing/season	8	0.28	0.24	1.22	0.47
Control versus 2 mowings/season	8	−0.78	0.24	3.22	**0.030**
1 mowing versus 2 mowings/season	8	−0.50	0.24	2.04	0.17
Years post-burn[b]	2, 2			0.78	0.51
Year	2, 1			14.56	**<0.001**

[a] Within-treatment comparisons were tested using the Tukey-Kramer comparison (i.e., mowing frequency and years post-burn).

[b] Within-treatment comparisons were not included for prescribed burning because the overall model was not significant, and the yearly differences were not significant.

burned shrublands and avoided shrublands that had been mowed ($\chi^2 = 14.43$, df = 2, $P < 0.001$; Fig. 1). As with Eastern Towhees, the frequency of mowing within a season had a significant effect on Common Yellowthroat presence ($\chi^2 = 17.47$, df = 2, $P < 0.001$), which was greater than expected in shrublands that had not been mowed, but lower than expected after one mowing; no Common Yellowthroats were recorded in shrublands that were mowed two or more times within a season.

Song Sparrow abundance did not differ among shrublands that had been mowed, burned, or left unmanaged ($\chi^2 = 1.97$, df = 2, $P = 0.37$; $\beta = 0.20$; Fig. 1). In addition, Song Sparrow presence did not change significantly with respect to the frequency of mowing ($\chi^2 = 1.66$, df = 2, $P = 0.44$). Neither Common Yellowthroat ($\chi^2 = 3.41$, df = 2, $P = 0.18$) nor Song Sparrow ($\chi^2 = 0.25$, df = 2, $P = 0.88$) presence differed with respect to years since burning.

Avian response to grassland management.—Within grassland areas, we recorded Savannah Sparrows, Song Sparrows, and American Goldfinches (*Carduelis tristis*). Savannah Sparrow abundance did not differ among grasslands that had been burned, mowed, or left unmanaged ($F_{2,4} = 0.04$, $P = 0.96$; $\beta = 0.06$; Fig. 2). Song Sparrow abundance was greatest in unmanaged grasslands (0.60/ha ± 0.09), but was similar in burned (0.11/ha ± 0.08) or mowed (0.11/ha ± 0.09; $F_{2,4} = 8.35$, $P = 0.025$) grasslands (Fig. 2).

DISCUSSION

Management in shrublands.—Our findings suggest that the effects of grassland restoration on generalist species will vary with management type and the subtle habitat preferences of the affected species. Not surprisingly, mowing produced the most noticeable changes in vegetation by reducing tall shrub cover. Mowed areas were dominated by litter and short shrubs and contained greater grass cover. Shrublands that were left unmanaged or burned once were not noticeably different and were characterized by tall shrubs. Due to logistical difficulties, such as the availability of adequate burn days and trained personnel, single burns are common in prescribed burning programs (Combs-Beattie and Steinauer 2001); thus, the results we observed in shrublands burned once could be expected in other prescribed fire programs.

Although several generalist species inhabited the same habitat type, a different suite of vegetation variables affected the presence of each species. Eastern Towhees were positively associated with litter and medium and tall shrubs (1.0–5.0 m), and they were negatively associated with medium-height grass. Common Yellowthroats preferred habitats characterized by no litter cover and medium-height shrubs (1.0–2.0 m). Song Sparrows preferred

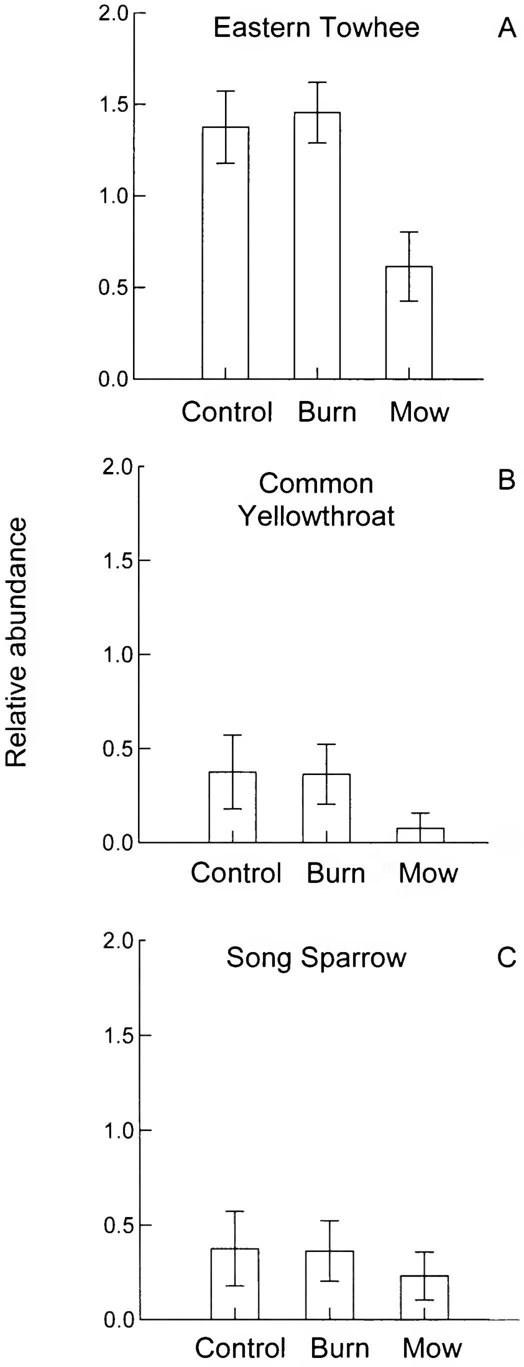

FIG. 1. In shrubland study sites, bird species responded differently to both burning and mowing management. The abundance (± 1 SE) of Eastern Towhees (A) and Common Yellowthroats (B) was most affected by mowing management, but was similar in burned and unmanaged shrublands. Song Sparrows (C) showed little response to management activities. Data collected on Nantucket Island, Massachusetts, 1999–2001.

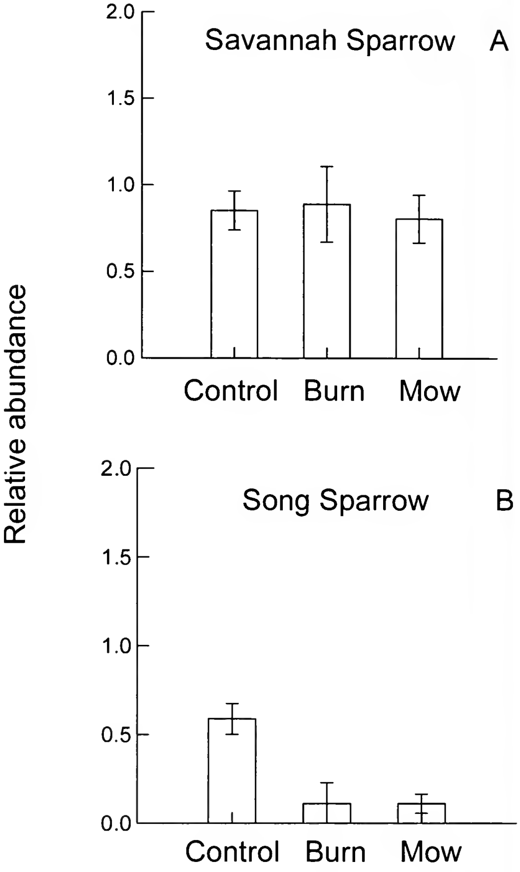

FIG. 2. In grassland study sites, Savannah Sparrow (A) densities (± 1 SE) were unaffected by management type, whereas Song Sparrow (B) densities (± 1 SE) were lower in both mowed or burned grasslands. Data collected on Nantucket Island, Massachusetts, 1999–2001.

areas that had grass and short shrub vegetation.

Despite being generalists, several bird species appeared to respond differently to burning and mowing treatments in shrublands, as has been found in other studies (e.g., Wiens and Rotenberry 1985, Wiens et al. 1986). Eastern Towhee and Common Yellowthroat densities were greater in shrublands that had been burned or left unmanaged, whereas Song Sparrow densities showed no response to either restoration technique (Fig. 1). The effects of mowing frequency were more immediate for Common Yellowthroats; they disappeared after the initial mowing event.

Grassland management.—In grassland habitats, prescribed burning and mowing produced similar results. The purpose of burning and mowing in grasslands was to maintain grassland. Consequently, management in grassland had less impact on vegetation structure than similar restoration techniques used in dense shrublands. Dunwiddie and Caljouw (1990) found that burning and mowing of Nantucket grasslands were equally effective in suppressing shrubs and enhancing grasses. In this study, unmanaged grasslands had greater cover of short shrubs compared with burned and mowed grasslands, and low-growing shrubs often dominated grasslands that were left unmanaged for >6 years (Dunwiddie and Caljouw 1990). Mowing resulted in grasslands with the greatest percentages of short- to medium-height grass cover. These findings suggest that, for a limited number of years, grasslands left unmanaged will continue to provide habitat for some species of grassland-dependent songbirds, but that eventually these grasslands will be succeeded by shrublands (Dunwiddie and Caljouw 1990).

Similar to shrubland generalists, the response of grassland generalists to management practices varied among bird species (Fig. 2). Savannah Sparrow abundance was similar in grasslands that had been mowed, burned, or left unmanaged. Song Sparrows, which were present in both grassland and shrubland habitats, occurred at significantly greater densities in unmanaged grasslands. Both Savannah and Song sparrows were negatively associated with litter and positively associated with medium to tall grass cover. Song Sparrows also were associated positively with short shrubs, whereas Savannah Sparrows were negatively associated with tall shrubs. Song Sparrows required short to medium shrubs, and any grassland management that substantially reduced shrub cover also reduced Song Sparrow abundance significantly.

Some researchers have suggested that site fidelity may preclude birds from responding immediately to management practices (Wiens and Rotenberry 1985, Wiens et al. 1986, but see Vickery et al. 1999). Our findings suggest that species-specific habitat requirements and the magnitude of the management, especially mowing, appeared to outweigh any affects of site tenacity for Common Yellowthroats and Eastern Towhees. The Eastern Towhee's preference for foraging habitat (i.e., litter; Greenlaw 1996) may make towhees less susceptible to burning and mowing than Common Yellowthroats. In the case of Song Sparrows, their lack of dependence on tall shrubs and their preference for grass cover may explain why their densities were not affected by either restoration technique.

The lack of avian response to management may have been a product of the spatial and temporal scales at which this study was conducted. Many avian species respond to habitat alteration at both landscape and patch scales (Herkert et al. 1994, Donovan and Flather 2002, McGarigal and Cushman 2002). The focus of our research, however, was patch-scale disturbances and responses, and not landscape-scale changes. In addition, many grassland birds are area-sensitive and require relatively large grassland habitats (>25 ha; Winter and Faaborg 1999, Mitchell et al. 2000, Johnson and Igl 2001). Because the average size of the grassland habitats included in this study was 13.4 ha (Table 1), many of the grassland areas may not have been large enough to support a diverse community of grassland birds, regardless of management intensity and/or duration. In the future, restoration activities within the shrubland study areas may produce relatively large grassland habitats, but our study was focused on the initial years of management as opposed to the long-term effects of restoration.

Management implications.—Conservation agencies must address several issues regarding the restoration or management of early-successional areas, including the response of generalist species and the type and spatial scale of the management. Despite sharing similar habitat requirements, individual bird species will respond differently to management due to subtle preferences in vegetation structure and composition. In the case of habitat restoration on Nantucket, much of the management had the unforeseen effect of making common species *less* common. Considering these species-specific responses to mowing and burning (even among habitat generalists), managers must proceed cautiously and consider the regional declines of the affected bird species. This is especially true of grassland restoration aimed at shrubland areas, as managers are faced with the dilemma of managing one regionally rare community at the expense of another. In this scenario, a dynamic and diverse set of strategies must be integrated into management such that sites are rotated, allowing some to succeed to later stages before they are disturbed, to provide habitat for both shrubland and grassland songbird communities.

ACKNOWLEDGMENTS

Logistical and financial support for this research was provided by the University of Massachusetts at Amherst, Massachusetts Audubon Society, Nantucket Conservation Foundation, Maria Mitchell Association, Partnership for Harrier Habitat Preservation, A. V. Stout Fund, Sweet Water Trust, Quebec Labrador Foundation, Conservation and Research Foundation, and National Fish and Wildlife Foundation. The Nantucket Conservation Foundation, Nantucket Land Bank Commission, and Nantucket Airport provided access to their properties. A. L. Jones, C. R. Griffin, D. E. Kroodsma, R. A. Askins, E. M. Steinauer, K. P. Combs–Beattie, R. Newman, J. F. Lentowski, E. F. Andrews, W. T. Maple, B. C. McComb, T. Hosmer, and K. McGarigal all provided helpful comments related to this study. F. M. Zuckerberg provided critical logistical support and is warmly acknowledged. We would like to thank D. H. Johnson and two anonymous reviewers for their thorough reviews of this manuscript.

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The Wilson Journal of Ornithology 118(3):364–373, 2006

SPATIAL BEHAVIOR OF EUROPEAN ROBINS DURING MIGRATORY STOPOVERS: A TELEMETRY STUDY

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ABSTRACT.—We studied the movement patterns of European Robins (*Erithacus rubecula*) at stopovers during spring and fall migration on the southeastern Baltic Coast, Russia. On the 1st, and sometimes the 2nd, day after arrival at a stopover site, robin movements were less aggregated than those made on subsequent days. Search/settling time varied between several hours and 2 days. During this period, migrants either occupied a defined stopover area or left the site. Stopover duration was 1 to 12 days in spring (mean = 2.4 days ± 0.31 SE) and 1 to 14 days in fall (mean = 3.4 days ± 0.50). The home-range size of European Robins on the southeastern Baltic Coast did not differ between seasons (spring: 4,320 m^2 ± 545, $n = 15$; fall: 3,562 m^2 ± 598, $n = 15$) and was similar to that at a central European site in fall (4,264 m^2 ± 241, $n = 14$). These home ranges were not defended territories. We found no relationship between the robins' spatial behavior and their fat stores on arrival, although in spring more lean than fat robins stopped for >2 days. The pattern of movements at the stopover was variable, both in birds that arrived lean and those that arrived with much more fat. Stopover duration estimates based on radio-tagging are superior to those based on capture-mark-recapture. *Received 27 December 2004, accepted 23 January 2006.*

Passerines spend at least 90% of their time during migration at migratory stopover sites. Stopover variables (e.g., rates of fat deposition, predation risk, habitat suitability) strongly influence migration strategies and tactics (Lindström 2003). Another important aspect of migrant stopover ecology is spatial behavior—territoriality versus broader movements, size of temporary home ranges, and sharing of home ranges versus defending them from conspecifics (Chernetsov 2003, Chernetsov and Bolshakov in press). Some migrants occupy temporary territories at stopovers (Rappole and Warner 1976; Kodric-Brown and Brown 1978; Bibby and Green 1980, 1981; Carpenter et al. 1983, 1993a, 1993b), whereas others move broadly across a given stopover area. Intraspecific variation in spatial behavior has also been reported; some individuals occupy relatively small home ranges, whereas others move over much broader areas (Aborn and Moore 1997, Delingat and Dierschke 2000). Until recently, capture-recapture analysis has been the main method for studying the pattern of movements made by passerines at stopovers (Titov 1999a, 1999b; Chernetsov and Titov 2001; Chernetsov 2002), and these analyses suggest that—during fall (southbound) migration—European Robins (*Erithacus rubecula*) occupy defined stopover areas (DSA). Robins spend up to 2 days occupying a DSA (Titov 1999a) and, after a maximum of 2 days, either resume migration or settle in a defined home range.

An important weakness of capture-recapture analysis is that the capture probability of passerine migrants at stopovers is usually low (Chernetsov and Titov 2000) and most likely differs between groups of birds (e.g., fat versus lean birds, those refueling versus those losing weight, and new arrivals versus those occupying a DSA). Radio-tracking has been used more recently (Aborn and Moore 1997, Lajda 2001), which makes it possible to ascertain the location of a bird without having to capture it or otherwise influence its behavior.

We investigated movement patterns of radio-tagged European Robins during spring (northbound) and fall migration stopovers on the southeastern Baltic Coast, Russia. Our objectives were (1) to test the hypothesis that individuals remain within defined areas at stopover sites; (2) to estimate home-range area and settling time; and (3) to assess the impact of initial fat stores on robins' spatial behavior. Understanding patterns of spatial use by migrants within habitats, including habitats being lost or fragmented, is crucial for understanding the importance of relatively

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TABLE 1. Number and condition of European Robins radio-tagged and followed during spring (northbound) and fall (southbound) migration stopover, 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia.

Season	No. tagged at stopover	No. followed from the 1st day	No. followed from the 1st to the last day	No. fat birds[a]	No. lean birds[a]
Spring					
2002	21	12	10	13	4
2003	30	30	29	16	14
Total spring	51	42	39	29	18
Fall					
2002	29	25	24	10	19
2003	36	36	35	17	19
Total fall	65	61	59	27	38

[a] Body mass of "lean" birds exceeded their calculated lean body mass by <1.2 g; body mass of "fat" birds exceeded their calculated lean body mass by >1.5 g.

large versus small habitat patches. Habitat use and spatial behavior of migratory landbirds have not been studied adequately, in spite of their importance as conservation issues (Petit 2000).

METHODS

Study site.—We conducted our study during spring and fall, 2002–2003, at Biological Station Rybachy on Cape Rossitten on the Courish Spit, Russia (southeastern Baltic coast, 55° 09′ N, 20° 51′ E). Our study periods were 1 April to 4 May 2002, 13 April to 7 May 2003, 2 September to 29 October 2002, and 6 September to 8 November 2003. The overall area of the study site is 6 ha. Vegetation at the study site is a mosaic of willow (*Salix* spp.) scrub and common reed (*Phragmites communis*), and some trees, including rowan trees (*Sorbus aucuparia*), white willows (*Salix alba*), and bird cherry (*Prunus racemosa*). We mist-netted European Robins—the most commonly occurring migratory species captured at this site (Bolshakov et al. 2002)—and banded them with aluminum leg-bands (Moscow Ringing Center bands).

Radio-tagged birds.—We fitted 117 European Robins with radio transmitters (Table 1). To obtain unbiased estimates of stopover duration, we made every effort to tag birds just after their arrival. The rate of daily captures of small passerines, including European Robins, at our study site are highly variable (due to occurrence of migration waves), as it is at many other coastal sites (Dolnik 1975, Titov and Chernetsov 1999, Chernetsov and Titov 2000). Results of seniority analysis (i.e., capture-mark-recapture models applied backwards in time; Pradel 1996) indicate that the vast majority of European Robins initially captured on days when many new birds are banded (following a day of few captures) have just arrived (Titov and Chernetsov 1999, Chernetsov and Titov 2000).

In 2003, all birds were radio-tagged on the 1st day of a migration wave ($n = 66$). In 2002, most European Robins were radio-tagged on the 1st day of a migration wave ($n = 37$), while others were radio-tagged upon recapture on the 2nd or 3rd day after their initial banding ($n = 13$). We assume that our estimates of stopover duration of tagged birds are unbiased.

All birds radio-tagged in fall were in their hatching year; in spring, all birds were in their 2nd calendar year. Bolshakov et al. (2003) used linear regression of body mass on wing length to calculate lean body mass of European Robins that had no visible subcutaneous fat (fat score 0, after Kaiser 1993); they made separate calculations for September, October (fall) and April (spring). Based on those calculations, all radio-tagged robins in our study were categorized as either "fat" or "lean" (Table 1); lean birds exceeded their calculated lean body mass by <1.2 g (<0.5 g in 63.4% of birds), and fat birds exceeded their calculated lean body mass by >1.5 g (>2.0 g in 93.8% of birds). If a bird was radio-tagged when recaptured rather than when it was first captured (which occurred in spring 2002), its fat score at the time of radio-tagging was used to assign it to the fat or lean group. The mass and wing length of birds at capture were recorded to the nearest 0.1 g and 0.5 mm, respectively.

Telemetry protocol.—We radio-tagged European Robins with LB-2 transmitters (Holohil Systems, Carp, Ontario, Canada). The measured life span of the transmitters was at least 10 days during spring passage and 21 days during fall migration. Transmitters were fitted as backpacks with a Rappole harness (Rappole and Tipton 1991). The weight of a transmitter with harness was 0.61 g, and the body mass of radio-tagged European Robins varied between 14.8 and 19.2 g; thus, the mass of transmitters represented 3.2–4.1% of a bird's body mass (<5% is believed to be the upper limit permissible; Caccamise and Hedin 1985, Naef-Daenzer 1993).

We used receivers with Yagi antennae from Wildlife Materials (Carbondale, Illinois) and Advanced Telemetry Systems (Isanti, Minnesota). The location of birds was estimated by biangulation and triangulation. For each individual, one location per hr was taken between the onset of daytime activity (dawn) and evening civil twilight. The number of observations per individual per day varied between 11 and 17, depending on the duration of the daylight period. Locations were plotted on a digitized map of the study area. From sunset to dawn, all birds were surveyed continuously from a stationary watch point 15 m above ground level; therefore, migratory departure time was usually detected to the nearest 1–3 min and the exact night of departure was known. Migratory departures invariably occurred during the nighttime. Generally, birds were absolutely stationary during the night (no signal change caused by movements); thus, an abrupt signal change indicated take-off. The signal could usually be received from the flying bird for some time (1–20 min), but it later disappeared. As the range of transmitter detectability did not exceed 1.5 km, signal reception from a flying bird for more than 3–4 min clearly indicated that a bird was flying in circles before choosing a direction. This behavior was very distinctive, and the probability that some other nocturnal activity was mistaken for a migratory departure was small. If a bird left the study area and occupied a home range elsewhere, the data for that bird were included only in qualitative estimates of whether or not the bird occupied a DSA. If a bird spent the night far enough from the stationary watch point to preclude signal reception at the stationary site, we attempted to locate it every 1–2 hr until dawn. A bird was assumed to have departed if the signal could not be detected during that night.

Data analyses.—We tested the locations for statistical independence by using the Schoener index (Swihart and Slade 1985). The data were not formally independent (i.e., consecutive locations were aggregated with a greater-than-chance probability); nevertheless, we assumed that our data could be used for the analysis of spatial distribution. We based our assumption on the empirical rule suggested by White and Garrott (1990), which states that if enough time has elapsed between two consecutive observations for an animal to move from one end of its home range to another, the observations in question may be considered statistically independent. In our study, at least 45 min elapsed between observations, during which each individual would have had ample time to move to any point in its stopover area.

When locating birds, every effort was made to approach them as closely as possible to minimize location error. We believe that in most cases we located their positions to the nearest 5 m and, following Lajda (2001), assumed a standard deviation of 10 m. Home-range area was estimated on the basis of all locations available as 95% kernel by Animal Movement Extension in ArcView (Hooge and Eichenlaub 2000). The estimated home-range area increases with an increasing number of locations until that number reaches 40–50 (Lajda 2001); therefore, we did not estimate the home-range area of birds with <38 locations. Due to this limitation, we only estimated home-range area for the entire stopover period and for the birds that stopped for >4 days ($n = 30$). To estimate the aggregation of locations from birds that were followed during shorter periods of time, we used the linearity index as applied in Animal Movement Extension of ArcView (Hooge and Eichenlaub 2000); this is the linear distance moved (i.e., the distance between the initial and final locations) divided by cumulative distance between all successive locations. The maximum value of the linearity index is 1 (i.e., if a bird is moving along a straight line). This index may be calculated for a given time interval

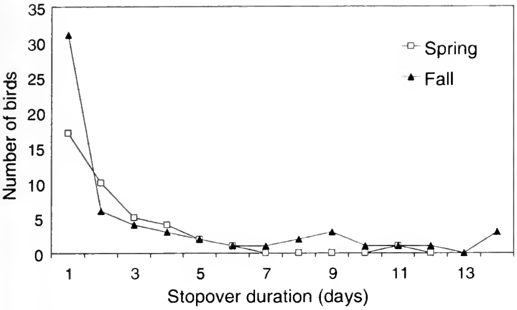

FIG. 1. Frequency distribution of stopover durations of European Robins assessed by radio tracking in spring (northbound) and fall (southbound), 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia. Only birds radio-tagged on the 1st day after arrival and known to depart by nocturnal flight are included. Spring: 2.4 days ± 0.31, median = 2, n = 40; fall: 3.4 days ± 0.50, median = 2, n = 59.

(e.g., the total observation period or a single day) and is a measure of area-restricted movement. The linearity index is reciprocal to the meander ratio (Williamson and Gray 1975) and was preferred to it due to the statistical properties of the linearity index. We used the arbitrarily selected threshold of 0.10 as an indication that a bird occupied a DSA; we assumed that birds showing linearity index values below this threshold remained in a DSA. For comparison, Aborn and Moore (1997) found that the meander ratio for Summer Tanagers (*Piranga rubra*) "settled" at stopovers on the Gulf of Mexico coast averaged 4.8, which corresponds to a linearity index of 0.21. Thus, our threshold was rather conservative.

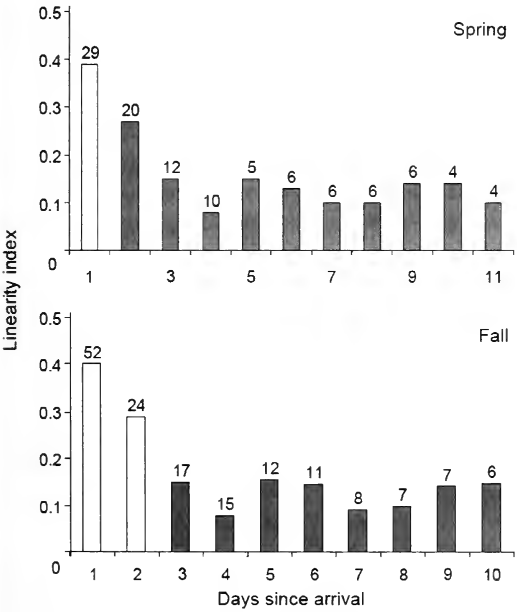

FIG. 2. Daily linearity index values of European Robins during spring (northbound) and fall (southbound) migration stopovers, 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia. Sample sizes are shown above the histogram bars. Days with mean linearity index values significantly different from the remaining days (one-way ANOVA with post-hoc tests) are shown by open bars.

We used t-tests to compare pairs of means when the assumption of population normality was not violated, and we used nonparametric Mann-Whitney U-tests when normality was clearly violated (e.g., distribution of stopover duration values, Fig. 1). We also used Spearman's rank correlation when the normality assumption was violated. We used ANOVA to compare multiple samples, and we used Tukey's honestly significant difference tests for post-hoc analyses. All tests were two-tailed; the null hypothesis was rejected if $P < 0.05$; means are presented ± SE. Data analyses were performed using SPSS version 11.0 (SPSS, Inc. 1999).

RESULTS

Spring Migration

Stopover duration and establishing a DSA.—The stopover duration of European Robins during spring migration varied from 1 to 12 days (Fig. 1). Twelve of 40 birds radio-tagged on the 1st day after arrival (30%) stopped for >2 days. The mean stopover length was 2.4 days ± 0.31.

We plotted the movements of 33 birds from the 1st until the last day of stopover. We obtained at least 6, and up to 92, locations over 1–6 days from these birds. The linearity index for these birds varied from 0.008 (very aggregated locations) to 0.65 (nearly straight-line movement) and was negatively correlated with both number of locations (Spearman's rank correlation: $r_S = -0.69$, $P < 0.001$) and stopover duration in days ($r_S = -0.58$, $P < 0.001$). The longer a bird remained at stopover, the more aggregated its locations were.

We also calculated the linearity index for each stopover day (Fig. 2). The pattern was rather obvious: during the 1st day of stopover,

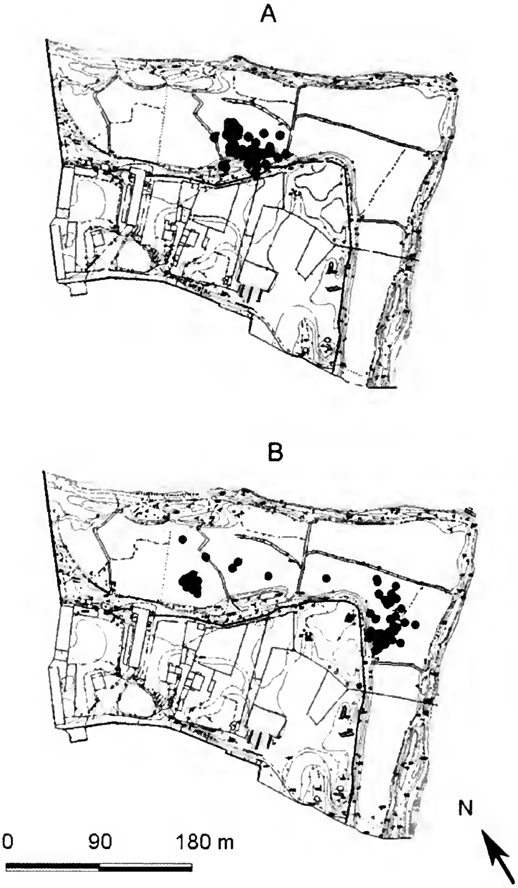

FIG. 3. Examples of the distributions of locations of two different birds during spring (northbound) and fall (southbound) migration stopovers, 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia. Each dot represents a single location. (A) All locations are in the defined stopover area (DSA). (B) Some locations are associated with the search/settling period; others are in the DSA.

robins moved broadly, and from the 2nd day on they began to remain in a more restricted area (one-way ANOVA: $F_{10,97} = 6.85$, $P < 0.001$). The linearity index for day 1 differed from that of all other days (Tukey's honestly significant difference test; all $P < 0.008$). For movements during the first day, the linearity index did not differ between birds continuing with migration on the 1st night and those that remained for more than 1 day ($t = 1.21$, $P = 0.20$, $n_1 = 14$, $n_2 = 15$). This means that on the 1st day of stopover, the birds behaved the same as they did on subsequent days: their movement patterns were not indicative of their subsequent decisions to remain or depart.

The movements of European Robins that remained for several days showed varying patterns. In some cases, all locations were aggregated (Fig. 3A). In others, first locations, presumably from the search/settling period, were more dispersed (Fig. 3B). We were able to estimate home-range area for 15 European Robins (where $n \geq 38$ telemetry locations; Table 2). DSA size was negatively correlated with the number of locations ($r = -0.54$, $P = 0.036$). Birds that stopped over for a long time (and thus yielded many location points) tended to remain within a more clearly defined area.

Behavior of fat and lean birds.—Of the 51 European Robins included in the analysis of spatial behavior, 18 were lean at radio-tagging (fat stores <0.5 g), 29 were fat (fat stores >2 g), and 4 had intermediate fat stores. The transmitter was removed from one lean bird, so its stopover duration was unknown. Of the remaining 17 lean birds, 10 (59%) stopped for >2 days, and mean stopover length was 3.8 days ± 0.75. The linearity index values of all these 10 birds were <0.10, and we assumed that they occupied a DSA. Of seven lean birds that stopped for 1–2 days, two remained with-

TABLE 2. Home-range size (m^2) of European Robins during spring (northbound) and fall (southbound) migration stopovers on the Courish Spit (Rybachy), southeastern Baltic Coast, Russia (this study) and during fall migration in southwestern Germany (Mettnau; Lajda 2001). There was no significant difference between Rybachy and Mettnau in fall ($t = 0.95$, $P = 0.35$) nor between seasons in Rybachy ($t = 0.94$, $P = 0.38$).

	Range (m^2)	Mean (m^2)	Median (m^2)	SE	*n*	Source
Spring, Rybachy	1,932–9,215	4,320	4,091	545	15	This study
Fall, Rybachy	1,060–10,083	3,562	2,801	598	15	This study
Fall, Mettnau	1,900–7,600	4,264	4,400	421	14	Lajda (2001)

in a small defined area, three roamed broadly, and two yielded too few locations to assign their spatial behavior as either DSA owners or roamers.

Of the 29 initially fat birds, seven (24%) remained for >2 days; the mean stopover duration was 2.6 days ± 0.53. All seven birds that stopped over for >2 days occupied a DSA. Of 21 birds that departed after 1–2 days, 11 moved broadly (linearity index >0.25). The difference in stopover duration between fat and lean birds was not significant (Mann-Whitney *U*-test: $z = 1.55$, $P = 0.12$); however, the proportion of birds that stopped for >2 days was greater among lean birds (Yates-corrected $\chi^2 = 4.15$, $P = 0.041$).

Home-range area in birds that arrived fat (4,101 m^2 ± 493, $n = 5$) and those that arrived lean (4,683 m^2 ± 976, $n = 8$) did not differ (*t*-test, $t = 0.44$, $P = 0.67$); however, we could only estimate home-range area in individuals that stopped over for ≥4 days. The linearity index did not differ between birds that arrived lean and those that arrived fat on either the 1st day of stopover (fat: 0.34 ± 0.039, $n = 16$; lean: 0.32 ± 0.059, $n = 11$; median test: $\chi^2 = 0.30$, $P = 0.58$) or on the 2nd day (fat: 0.18 ± 0.037, $n = 11$; lean: 0.15 ± 0.040, $n = 6$; median test: $\chi^2 = 0.03$, $P = 0.86$). Apparently, both lean and fat birds can show various spatial patterns in the first days after arrival. We did not compare linearity indices of initially lean and initially fat birds in the subsequent (>2) days after arrival, because the chance was too high that the nutritional status of the birds had already changed.

Fall Migration

Stopover duration and establishing a DSA.—Fall stopover duration varied between 1 and 14 days (Fig. 1). Twenty-three European Robins of the 59 tracked since the 1st day of stopover remained over for >2 days. The mean stopover length was 3.4 days ± 0.50 (Fig. 1), which did not differ significantly from the duration of spring stopovers (2.4 days ± 0.31; Mann-Whitney *U*-test: $z = 0.03$, $P = 0.97$).

Of the birds that stopped for >2 days ($n = 23$), all but one occupied a DSA. One bird that stopped for 3 days in fall 2003 covered a linear distance of ~4 km, moving during daytime before it departed. Home-range size was estimated for 15 individuals for which at least 39 locations were obtained per bird (Table 2). The number of locations was not significantly correlated with home-range size ($r = -0.43$, $P = 0.11$). The area of DSAs occupied during fall migration did not differ significantly from the area of DSAs occupied in spring (Table 2).

In fall, European Robins spent from several hr to 1.5 days moving around before settling. In one case, a European Robin that settled in a DSA on the 1st day changed its DSA on the morning of the 4th day. This individual departed by nocturnal flight after a 5-day stopover.

We tracked 42 birds from the 1st until the last day of stopover. We obtained 4–172 locations over 1–14 days from these birds. The linearity index of their movements varied from 0.003 to 0.93 and was negatively related to both number of locations (Spearman's rank correlation: $r_S = -0.55$, $P < 0.001$) and stopover duration in days ($r_S = -0.56$, $P < 0.001$). Individuals that stopped over for longer periods showed more area-restricted movement.

In fall, the linearity index differed between the days of stopover (one-way ANOVA: $F_{9,149} = 6.69$, $P < 0.001$). The days with linearity index values different from the others were days 1 and 2 (both different from, e.g., day 4, Tukey's honestly significant difference test: $P < 0.001$ in both cases). Beginning with the 3rd day of stopover, there was no significant between-day variation in the linearity index (post-hoc tests; all $P > 0.05$). The linearity index did not differ between the 1st and the 2nd day of stopover (Tukey's HSD test: $P = 0.56$). On the 1st day, the linearity index did not differ between birds continuing migration on the next night and those that remained for more than 1 day ($t = 0.97$, $P = 0.34$, $n_1 = 28$, $n_2 = 27$).

Behavior of fat and lean birds.—Of 65 European Robins radio tracked in fall, 38 were lean when radio-tagged and 27 were fat (Table 1). Of the 38 lean birds, 19 (50%) stopped over for >2 days. Mean stopover duration was 4.1 days ± 0.67 (median = 2 days, $n = 36$); for two birds, stopover duration was not known exactly, but was >2 days. Of the 19 lean robins that stopped over for >2 days, 18 occupied a DSA (linearity index <0.10). The only bird with a higher linearity index (0.22), stopped for 3 days. Of the 19 lean birds that spent 1–2 days at the stopover, the movements of 10 were not very area-restricted (linearity index >0.25). Of the 27 initially fat robins, 9 (33%) stopped for >2 days, and mean stopover duration was 3.2 days ± 0.69 (median = 1 day). The difference in stopover duration between fat and lean birds was not significant (Mann-Whitney *U*-test: $z = 0.74$, $P = 0.43$). The difference in the proportion of fat and lean birds that stopped over for >2 days also was not significant (Yates-corrected $\chi^2 = 1.17$, $P = 0.28$).

As in spring, there was no difference in the size of DSAs between initially fat (2,970 m^2 ± 518, $n = 6$) and initially lean (3,957 m^2 ± 939, $n = 9$) birds ($t = 0.80$, $P = 0.44$). Stopover area could be estimated only for robins that made longer stopovers (>4 days), during which their nutritional status might have changed. All birds that carried large fat stores at arrival and stopped over for >2 days ($n = 9$) occupied a DSA. The linearity index was <0.10 in all cases in which it was possible to calculate ($n = 6$). Fat robins that stayed for 1–2 days ($n = 19$) moved across a large area (linearity index >0.25 in 10/14 cases). Five birds were tracked for too short a time to estimate their spatial status.

DISCUSSION

Even though the maximum stopover duration assessed by radio tracking was 12 days in spring and 14 days in fall, the medians were 2 days and 1 day, respectively. In spring and in fall, 70% and 61%, respectively, of European Robins resumed migration after 1 or 2 days of stopover. Even though there was a weak tendency among lean birds to make longer stopovers, it was not statistically significant. Optimal migration theory predicts that in time-minimizing migrants, stopover duration should depend on migrant fuel status and fat-deposition rate (Alerstam and Lindström 1990). Wind direction and strength are also of paramount importance (Liechti and Bruderer 1998). Our data, like that of some other studies (e.g., Rguibi-Idrissi et al. 2003), indicate that relationships between individual stopover parameters (e.g., stopover duration and fat status) are often not as straightforward as predicted by the necessarily simplified models.

Our telemetry study of European Robins at a migratory stopover showed that all birds that stopped over for >2 days occupied a DSA. Previously, this pattern has been predicted on the basis of capture-recapture analysis (Szulc-Olech 1965, Titov 1999b); however, analysis based on recaptures is an indirect method that is strongly dependent on the recapture probabilities of the birds. Our telemetry data, which are independent of recapture probability, confirmed the hypothesis that European Robins first move around broadly, and, after 1–2 days, either settle in a DSA or resume migration. During the first 2 days after arrival, roughly one-half of the birds remained within a restricted area and one-half moved broadly (high linearity index). The latter pattern was especially typical of the 1st day after arrival. The maximum linear range of European Robin movements was ~4 km. We suggest that these movements were associated with the search/settling period when fat-deposition rates may have been low or even negative (Titov 1999a, Chernetsov et al. 2004b). Normally, positive fat-deposition rates are not achieved until the birds settle and occupy a DSA (Titov 1999a).

Direct visual observations of radio-tagged European Robins suggested that their DSAs were not defended territories, either in spring or in fall. We frequently observed "intruders" in the core parts of occupied home ranges, quite near the owner and causing no aggression. In the vast majority of cases, Lajda (2001) observed no aggressive responses to a mounted European Robin presented to DSA owners during migration. In our study, home ranges of neighbors often overlapped, a pattern also reported by Lajda (2001). Territorial behavior in birds is known to be context-dependent (Davies and Houston 1983) and might or might not occur, depending on food distribution and availability, density of competitors, or exposure to predators. Although we did not observe territorial behavior in European Robins during migratory stopovers, we cannot rule out that, in some situations (e.g., low density of conspecifics), they might be territorial at stopovers. The DSA size used by European Robins during fall migration stopovers at Cape Rossitten did not differ between seasons (Table 2). The size of home ranges occupied during fall stopovers on the Courish Spit did not differ from the values reported from the Mettnau peninsula in southwestern Germany (Lajda 2001). It is worth noting, however, that fall stopovers at Rybachy (3.4 days ± 0.50) were significantly shorter than those reported in southwestern Germany (6.7 days ± 1.04, Mann-Whitney U-test: $z = 2.79$, $P = 0.003$; Lajda 2001).

In our study, European Robins spent up to 2 days settling. Two days seems to be the maximum length of search/settling time, after which a robin must either establish a DSA, or leave the area. Our estimate of search/settling time, an important stopover parameter for optimal migration models (Weber and Houston 1997a, 1997b; Houston 1998; Chernetsov et al. 2004b), ranges from several hours up to 2 days. In some cases, birds that seemed to have occupied a DSA for several days would then move up to 1 km and occupy a new DSA. Even though settling within 2 days is a general rule for migrating European Robins, there may be exceptions.

We did not find a relationship between spatial behavior of European Robins and their fat stores on arrival. The only difference was that, in spring, more lean birds than fat birds stopped for >2 days. Because fat status of migrants is known to affect their foraging behavior (Loria and Moore 1990), which is closely related to spatial behavior, we had expected a difference in average stopover duration. The pattern of movements at the stopover could have been quite varied in either group. It is most likely that during stopover the fat stores of the birds changed: most individuals probably refueled, but some may have lost mass, especially during the initial phase of stopover, as observed by Rappole and Warner (1976), Moore and Kerlinger (1987), Moore and Yong (1991), and Yong and Moore (1997). European Robins that stopped over for longer periods probably gained mass, but the low number of recaptures after >3–4 days of stopover precluded us from estimating fat-deposition rates.

The proportion of birds stopping over for >2 days (30% in spring and 39% in fall) was much greater than that estimated by capture-mark-recapture models (8.4% for birds first captured during a wave of arrivals; Chernetsov and Titov 2000). The reason for this disagreement is probably not a delayed departure due to the effect of radio-tags (our study), but the fact that birds that leave the immediate vicinity of the release site—but remain within 500–1,000 m—are assumed in capture-mark-recapture estimates to have departed. We suggest that capture-mark-recapture estimates, and not the estimates based on telemetry data, are biased.

Occupation of DSAs, which we found in the European Robin—or occupation of territories, as reported by a number of authors for several other passerine species (Rappole and Warner 1976; Kodric-Brown and Brown 1978; Bibby and Green 1980, 1981)—is just one possible tactic employed by migrants at stopovers. Other nocturnal passerine migrants, for example, Blackcap (*Sylvia atricapilla*; Chernetsov 2002), Sedge Warbler (*Acrocephalus schoenobaenus*; Bibby and Green 1981, Chernetsov and Titov 2001), and Eurasian Reed Warbler (*A. scirpaceus*; Chernetsov and Titov 2001), occupy larger areas than do robins. In some species, authors have observed birds making broad movements, and in others they have observed birds occupying DSAs or even defending territories—e.g., the Pied Flycatcher (*Ficedula hypoleuca*; Bibby and Green 1980, Chernetsov et al. 2004a) and the Eurasian Reed Warbler (Bibby and Green 1981, Chernetsov and Titov 2001). Interspecific comparisons suggest that spatial pattern and territorial behavior of stopover migrants are probably related to the pattern of food distribution (Chernetsov and Bolshakov in press) and possibly to the density of conspecific and heterospecific competitors. European Robins forage mainly on terrestrial invertebrates, which are relatively evenly distributed across space and time (Titov 2000, Chernetsov and Titov 2003), and may occupy a DSA, at least when they make a longer stopover. Species whose prey are more unpredictable (e.g., Eurasian Reed and Sedge warblers, Chernetsov and Titov 2001; Pied Flycatchers, Chernetsov et al. 2004a), move more broadly.

ACKNOWLEDGMENTS

The authors are grateful to D. Leoke for his help in the field and to W. Fiedler for logistical assistance. Constructive criticism by three anonymous reviewers helped to improve an earlier draft. This study was supported by the Russian Foundation for Basic Research (grant no. 02-04-48608).

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The Wilson Journal of Ornithology 118(3):374–379, 2006

AGE-RELATED TIMING AND PATTERNS OF PREBASIC BODY MOLT IN WOOD WARBLERS (PARULIDAE)

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ABSTRACT.—We compared timing and patterns of prebasic body molt between hatch-year (HY) and after-hatch-year (AHY) American Redstarts (*Setophaga ruticilla*) and Yellow Warblers (*Dendroica petechia*) in Ontario, Canada. In each body region of both species, there was no age-related difference in the proportion of individuals undergoing molt. Furthermore, there was no difference between HY and AHY American Redstarts in the overall timing of body molt; molt started in early July and lasted until early September. In contrast, HY Yellow Warblers started body molt in late June to early July, while adults began body molt in mid-July. Both American Redstarts and Yellow Warblers displayed age-class differences in the intensity and timing of molt among specific body regions. External factors (e.g., food availability and geographical distribution), and internal factors (e.g., physiological status) may contribute to variations in body molt timing observed in these two species.
Received 2 December 2004, accepted 13 March 2006.

Molt plays an important role in the life cycle of birds because feathers have multiple functions, such as display during courtship (e.g., Beehler 1983), thermoregulation (Schieltz and Murphy 1997), and protection from dermal parasites (Post and Enders 1970). Most importantly, birds must replace their feathers before progressive wear impedes flight (Ginn and Melville 1983). However, molting consumes large amounts of energy and protein reserves to produce new feathers and to compensate for the effects of reduced insulation and decreased flight efficiency (Dolnik and Gavrilov 1979; Murphy and King 1991, 1992). To minimize energetic constraints and avoid undue overlap with other energetically demanding activities, such as reproduction and migration, many birds molt during times when food is abundant (Payne 1972).

Typically, adult (after-hatch-year or AHY) wood warblers attain basic plumage by undergoing a complete prebasic molt—which replaces nearly all feathers—while still on the breeding grounds prior to migration. Hatch-year (HY) wood warblers with juvenal plumage body feathers—which are weaker and looser in texture—attain their winter plumage through a first prebasic molt, replacing only body contour feathers and most of the wing coverts (Pyle 1997).

After breeding, most warblers prepare for the flight to their wintering grounds by increasing their nutritional intake and molting prior to migration. We compared the body molt patterns and timing of HY versus AHY Yellow Warblers (*Dendroica petechia*) and American Redstarts (*Setophaga ruticilla*) to determine whether any age-related differences in chronology and rate of molt could be attributed to constraints inherent to the breeding cycle. HY warblers do not molt as extensively as AHYs; hence, their preparations for migration, including molt, may be limited by the timing of fledging. Thus, we would expect AHYs—constrained by both nesting responsibilities and the timing of migration—to begin molting later than HYs but, once initiated, to undergo a more rapid body molt.

METHODS

Study areas.—Yellow Warbler and American Redstart molt data were obtained at Innis Point Bird Observatory (IPBO) and Thunder Cape Bird Observatory (TCBO), respectively. IPBO is located approximately 12 km west of Ottawa, Ontario (45° 22′ N, 75° 53′ W) near Shirley's Bay on Department of National Defense property along the southwestern bank of the Ottawa River. The surrounding habitat includes deciduous forest and regenerating farm fields dotted with small trees and shrubs. TCBO is situated at the tip of the Sibley Peninsula, on the northwest shore of Lake Supe-

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rior, approximately 80 km from Thunder Bay, Ontario (48° 18′ N, 88° 56′ W). The area is predominantly forested, consisting mostly of coniferous trees and shrubs.

Field procedures.—From 6 July to 10 September 1998–2002, we captured 113 American Redstarts (85 HYs and 28 AHYs) and 68 Yellow Warblers (43 HYs and 25 AHYs) using mist nests (30-mm mesh size) and Heligoland traps according to TCBO and IPBO standard protocols. Ninety-four American Redstarts (71 HYs and 23 AHYs) and 50 Yellow Warblers (27 HYs and 23 AHYs) were actively molting when captured. We obtained body molt data for five body regions (head, back, belly, uppertail coverts, and undertail coverts). To satisfy sample size and distribution requirements of log-linear models (Sokal and Rohlf 1995, Yuri and Rohwer 1997), each body region was scored on an ordinal scale of 0 to 5 based on the estimated proportion of actively molting feathers (molt score of 0 = no molt; 1 = 0–20% complete; 2 = 21–40%; 3 = 41–60%; 4 = 61–80%; and 5 = 81–100%). A total body molt score for each individual was determined by summing the individual molt scores for all five body regions; thus, total body molt scores ranged from 0 to 25. To obtain a representative sample, body molt was scored on all birds captured, whether they were molting or not.

AHY warblers were differentiated from HY warblers on the basis of plumage and bill color, and extent of skull pneumatization. HY Yellow Warblers are typically duller in coloration than AHYs in definitive basic plumage, and they have tapered outer primary coverts with narrow or indistinct buffy edging (Pyle 1997). Also, AHYs have dark lower mandibles (Mundy and McCracken 1997). Female AHY American Redstarts were distinguished from HYs of both sexes by their truncate, dusky brown outer primary coverts (not tipped with buff) and the large yellow patch on their rectrices. In addition, the AHY's outer rectrices of both species have truncated inner webs. AHYs were also identified by their fully pneumatized skulls; skulls of HYs were incompletely pneumatized (Pyle 1997).

Statistical analyses.—We categorized capture dates for American Redstarts into three consecutive, 17-day blocks (22 July to 7 August: n = 21 HYs and 12 AHYs; 8 to 24 August: n = 45 HYs and 9 AHYs; 25 August to 10 September: n = 5 HYs and 2 AHYs). To satisfy sample size and distribution requirements of log-linear models (Sokal and Rohlf 1995, Yuri and Rohwer 1997), molt scores of 0 to 1 were combined. Capture dates for Yellow Warblers were divided into three consecutive, 16-day blocks to provide a feasible distribution of captures (6 to 21 July: n = 13 HYs and 3 AHYs; 22 July to 6 August: n = 8 HYs and 9 AHYs; 7 to 22 August: n = 6 HYs and 11 AHYs). Due to an unequal distribution of molt scores among body regions, molt scores were grouped into only three classes (0–3, 4, and 5).

To determine peak molt interval and the progression and rate of molt, we first ran log-linear models with a G-test using Williams' correction (Sokal and Rohlf 1995) to determine whether overall body molt scores (i.e., five body regions; for HY and AHY warblers) were independent of capture date (i.e., three consecutive 17-day blocks for American Redstarts, 16-day blocks for Yellow Warblers; Yuri and Rohwer 1997). We then used one-way analyses of covariance (ANCOVA; Sokal and Rohlf 1995)—using total body molt score as the dependent variable, age as the independent variable, and date captured as the covariate—to test for age class differences in the timing of body molt (all body regions combined). We used SPSS (Release 10.07a) for Macintosh (SPSS, Inc. 2000), and set statistical significance at $P < 0.05$.

RESULTS

Yellow Warblers.—Body molt of all regions occurred from early July to mid-August. Within this period, molt progressed uniformly with no peak interval, which would have been expressed as a greater proportion of individuals undergoing molt. For example, whether age classes were pooled or analyzed separately, there was no difference in the proportion of molting individuals with respect to date (G-tests: $P > 0.99$ in all cases).

The timing of body molt depended on age; HYs began body molt earlier than AHY individuals ($F_{1,49} = 11.23$, $P = 0.002$, $n = 50$; Fig. 1). Molt scores across body regions differed between age classes ($G_{\text{adj}} = 16.49$, df = 8, $P < 0.05$); the greatest differences were observed in the crown (HY mean molt score

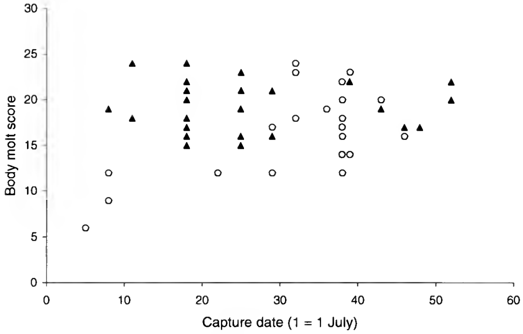

FIG. 1. Relationship between total body molt score and capture date (6 July to 22 August) for hatch-year (HY; triangles) and after-hatch-year (AHY; circles) Yellow Warblers. HY birds typically began molt earlier than AHY individuals ($F_{1,49}$ = 11.23, P = 0.002).

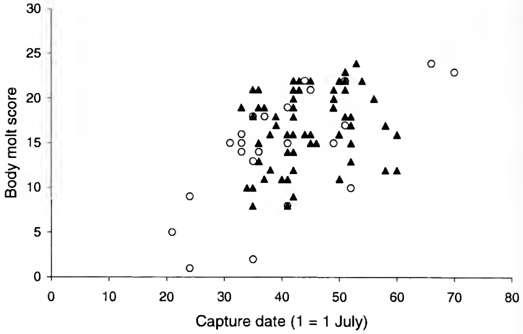

FIG. 2. Relationship between total body molt score and capture date (22 July to 10 September) for hatch-year (HY; triangles) and after-hatch-year (AHY; circles) American Redstarts. The timing of molt did not differ between HY and AHY birds ($F_{1,93}$ = 1.34, P = 0.25).

= 4.4; AHY mean molt score = 3.5) and back (HY mean molt score = 4.0; AHY mean molt score = 3.4) regions. The progression of body molt for HY individuals was crown, back, undertail coverts, uppertail coverts, and belly; for AHY birds, the sequence was undertail coverts, uppertail coverts, crown, back, and belly. In both age classes, undertail and uppertail covert molt occurred almost simultaneously.

With respect to timing, molt scores differed between age classes (G_{adj} = 17.74, df = 4, $P < 0.005$). The greatest difference occurred from 6 to 21 July, during which the estimated mean molt score (i.e., mean value of the molt score for all five body regions) was 3.9 for HYs and 3.0 for AHYs, indicating that molt begins earlier among HYs than among AHYs during that date block. From 22 July to 6 August, HY body molt decreased slightly (mean molt score 3.8), but in AHYs it increased (mean AHY molt scores in time blocks 1, 2, and 3 were 3.0, 3.7, and 3.8, respectively).

From 6 to 21 July, the percentage of individuals that had not started molting (molt score 0) was 33% for HYs and 35% for AHYs. By 22 July, however, all individuals had initiated molt. By date block, the percentage of individuals that had completed their molt (molt score 25) was 0% for both age classes (6 to 21 July), 47% for HYs and 0% for AHYs (22 July to 6 August), and 25% for HYs and 0% for AHYs (7 to 22 August). All AHYs were in active body molt from 22 July to 22 August; however, AHYs captured from 7 to 22 August had total molt scores of 23 or 24, indicating that their molt was almost completed by then.

American Redstarts.—Body molt in all regions occurred from mid-July to early September. Whether age classes were pooled or analyzed separately, there was no age-class difference in the proportion of individuals undergoing body molt (G-tests: $P > 0.50$ in all cases).

Analyses of the effect of age class—with total body molt score as the dependent variable and capture date as a covariate—indicated no difference in timing of molt within any date block ($F_{1,93}$ = 1.34, P = 0.25, n = 94; Fig. 2). Although body molts in HYs and AHYs were concurrent, molt scores across body regions differed between age classes (G_{adj} = 79.17, df = 16, $P < 0.001$): HY molt was more advanced than that of AHYs in all three date blocks. The greatest difference in molt scores between age classes was in the undertail covert region (mean HY molt score = 3.6; mean AHY molt score = 3.1). The progression of body molt for HYs was back, undertail coverts, uppertail coverts, belly, and crown; for AHY birds it was back, uppertail coverts, undertail coverts, belly, and crown. In both age classes, undertail coverts and belly molts occurred almost simultaneously.

With respect to timing, American Redstarts displayed age-related differences in molt scores (G_{adj} = 42.14, df = 8, $P < 0.001$). From 25 August to 10 September, there was a large age-related difference in molt scores; the estimated mean molt score (i.e., mean value of the molt score for all five body regions) was 3.2 for HYs and 4.6 for AHYs, indicating that AHYs initiate molt earlier than HYs during that date block. In addition, body molt of HYs was most intense in early August (mean molt score 3.6); however, in AHYs it increased linearly with time (mean molt scores in time blocks 1, 2, and 3 were 2.5, 3.2, and 4.6, respectively).

Within the three date blocks, the percentage of individuals that had not initiated molt (molt score 0) was 0% for HYs and 20% for AHYs (22 July to 7 August), 2% for HYs and 0% for AHYs (8 to 24 August), and 0% in both age classes (25 August to 10 September). The percentage of individuals that had completed molt (molt score 25) was 4% for HYs and 0% for AHYs (22 July to 7 August), 16% for HYs and 0% for AHYs (8 to 24 August), and 38% for HYs and 50% for AHYs (25 August to 10 September). All AHYs were actively molting from 8 to 24 August.

DISCUSSION

Ginn and Melville (1983) emphasized the need to examine body molt because body feathers account for more than half of a bird's feather mass. Consequently, their replacement may lead to greater overall energetic requirements than the molt of flight feathers. Molt must be timed to minimize energetic losses while progressing adequately enough to prepare for fall migration; thus, a bird's annual cycle must be structured to optimize reproductive, migratory, and molt requirements. Factors such as arrival on the breeding grounds will set the timeline that AHY warblers require to fulfill all the tasks associated with breeding. On the other hand, the molt timeline for HY birds is probably established by hatch dates, with factors such as nutritional provisioning by adults determining the optimal physiological conditions for molt. Furthermore, to maximize flight efficiency, both age classes must complete adequate feather replacement prior to departure for the wintering grounds.

Molt in relation to breeding.—One may assume that HY warblers would be more likely to initiate molt earlier than AHY birds because they do not expend time or energy producing offspring. In addition, the first prebasic molt of wood warblers does not include most of the flight feathers (Pyle 1997); hence, physiological demands of feather replacement in HY birds should be considerably less than that of AHY individuals. As predicted, our study demonstrates that HY Yellow Warblers do initiate molt earlier than AHYs. Body molt began in late June to early July for HYs and mid to late July in AHYs, with greatest age-related differences in molt scores occurring in the 6 to 21 July date block. In Ontario, records of active Yellow Warbler nests peak during the first 2 weeks of June (Peck and James 1987), suggesting that HY birds may begin prebasic body molt while still in the nest. Lowther et al. (1999) also indicated that prebasic molt in Yellow Warblers often begins before fledging. Peak fledging of Yellow Warblers in Ontario occurs in late June (Peck and James 1987). Our early captures demonstrated that body molt in most HY Yellow Warblers was well underway during the first week of July; 67% of individuals were in active molt and had a mean molt score of 3.9.

Differences in body molt schedules in Yellow Warblers relative to ongoing energetic expenditures other than molt also may explain differences observed in molt intensity over time. For example, in early to mid-July, HY birds had considerably higher molt scores than AHYs for all body regions combined. Molt in AHY Yellow Warblers overlapped with breeding; consequently, they may be compensating with a less intensive body molt early in the molting period. Nolan (1978) suggested that Prairie Warblers (*Dendroica discolor*) with dependent young underwent slower molt than birds that were not tending to offspring. Our results showed increased molt intensity in AHYs in mid-to late July when young are less dependent on their parents (Lowther et al. 1999). At James Bay in northern Ontario, Rimmer (1988) concluded that molt among Yellow Warblers typically overlaps fledgling care because the young are relatively independent at that time, thereby reducing parental demands.

We found that body molt for both age classes of American Redstarts occurred concurrently in all body regions from mid-July to early September. Other warbler species, including Hermit (*Dendroica occidentalis*) and

Townsend's (*D. townsendi*) warblers, also display a lack of age-related differences in the timing of body molt (Jackson et al. 1992). Similar to that of Yellow Warblers, body molt in AHY American Redstarts overlapped with breeding. In Ontario, records imply that peak fledging of American Redstarts occurs during mid-to late June (Peck and James 1987); therefore, young would continue to be dependent on parents through July (Sherry and Holmes 1997). The parallel timing of body molt between HY and AHY American Redstarts could explain the similarities in their molt intensity during the first month of the molt period, in which case the adult birds must have sufficient energetic reserves to complete their parental duties when initiating molt. However, the considerable age-related difference in molt intensity from 25 August to 10 September might reflect the termination of breeding duties, allowing for more energy to be allocated to the molting process.

Molt in relation to migration.—Most migratory birds complete a substantial portion of their prebasic molt before leaving the breeding grounds; some warbler species delay their departures for several days until their feathers are adequately grown (Rimmer 1988). It has been shown that body molt and primary feather molt can occur simultaneously (Sherry and Holmes 1997, Lowther et al. 1999). Furthermore, the rate and chronology of primary molt in many species of wood warblers are typically correlated with time of southbound migration, such that earlier departure from the breeding grounds is associated with a shorter and more rapid molt (Debruyne 2003).

Yellow Warblers are among the earliest of wood warblers to begin their southbound migration, with most departing from their breeding grounds in eastern Canada by early August (Lowther et al. 1999). Peak migration of HY individuals may occur 1–2 weeks earlier (Rimmer 1988). This is consistent with our study, which demonstrates that body molt occurs earlier in Yellow Warblers than it does in American Redstarts, which begin migration in late August to early September (Sherry and Holmes 1997), and that molt in HY Yellow Warblers occurs earlier than it does in AHY individuals. HY birds would be able to molt and migrate earlier than AHYs because they do not have the energetic demands of raising young and their first prebasic molt does not include most of the flight feathers. Furthermore, both HY and AHY Yellow Warblers may begin migrating while undergoing the final stages of body molt. Rimmer (1988) noted that AHY Yellow Warblers in northern Ontario begin migrating during the final stages of molt (i.e., final stages of growth of the last two primaries); he suggested that the energetic costs associated with this stage of molt were not significant enough to preclude simultaneous migration. Rimmer also found that Yellow Warblers lost body weight during the later stages of molt because individuals departed without the typical premigration accumulation of fat. He concluded that migration timing may be regulated by flight efficiency rather than physiological readiness. This relief from the constraint of premigratory preparedness would favor an early departure from the breeding grounds, particularly if suitable food resources are exhausted.

The timing of body molt for HY and AHY American Redstarts at TCBO is consistent with the timing of southbound migration in late August; many individuals had completed body molt by this time. Additionally, both age classes arrive synchronously at the banding stations of LPBO and the Allegheny Front Migration Observatory in West Virginia (Hall 1981, Woodrey and Chandler 1997). This supports the lack of age-related differences in the timing of prebasic molt among American Redstarts. Jackson et al. (1992) observed that male Hermit and Townsend's warblers complete most of their prebasic molt on their breeding grounds prior to migration, and suggested that their breeding areas—moist montane and lowland habitats, respectively—still provided sufficient food resources after breeding to allow birds to molt before departure. American Redstarts also prefer moist, productive habitats that offer abundant food resources in late summer (Sherry and Holmes 1997), perhaps explaining similarities in the timing of molt among these species. In addition, American Redstarts demonstrate substantial flexibility in both dietary choices and foraging strategies, which would allow both HY and AHY individuals to linger on the breeding grounds during molt.

This study provides a foundation for future research on body molt in two wood warbler species found throughout eastern North America. External factors, including food availability, and internal factors, such as physiological readiness to molt and migrate, may provide some explanation for the timing of body molt. Continued examination of the many biological and environmental aspects affecting molt and migration will contribute to a better understanding of body molt patterns in wood warblers.

ACKNOWLEDGMENTS

We thank the staff and volunteers at Thunder Cape and Innis Point bird observatories for collecting molt data over many years; this study would not have been possible without their long hours of hard work. The senior author is particularly grateful to J. Allair, J. Woodcock, M. Woodcock, K. Burrell, P. Biedermann, C. Friis, and A. Blake for their assistance with her field work at Thunder Cape in 2002. The Thunder Cape Bird Observatory is a joint project of the Thunder Bay Field Naturalists, Bird Studies Canada, and the Ontario Ministry of Natural Resources (OMNR), with major funding from OMNR's Wildlife Assessment Program. We would also like to thank C. C. Rimmer and two anonymous reviewers for their helpful suggestions. This research was supported, in part, by a Natural Sciences and Engineering Research Council grant to JMH. This paper is a contribution of the Ontario Ministry of Natural Resources, Wildlife Research and Development Section.

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The Wilson Journal of Ornithology 118(3):380–390, 2006

FORAGING ECOLOGY OF BALD EAGLES AT AN URBAN LANDFILL

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ABSTRACT.—We observed Bald Eagles (*Haliaeetus leucocephalus*) foraging at the landfill in Vancouver, British Columbia, Canada, 1994–1996 and 2001–2002, to determine (1) diet and time budgets of eagles visiting the landfill; (2) whether food taken from the landfill provided a significant energy source for local eagle populations; and (3) the effects of eagle density and weather on eagle behavior. Eagles fed primarily on human refuse (95%, $n = 628$), but food items taken from the landfill accounted for only 10 ± 3% of their daily energy needs. Subadults foraged at the landfill more often than adults, and most "refuse specialists" appeared to be subadults. Eagle time budgets consisted of mostly resting (91%), the remainder largely spent drinking (2.6%), scavenging (2.3%), and pirating (1.8%). Resting increased with wind speed, and foraging efficiency declined with precipitation, consistent with the hypothesis that the landfill is primarily a location for resting during inclement weather. Foraging efficiency decreased when number of eagles and piracies increased, and percent of eagles foraging decreased with increased numbers of eagles. The home ranges of only 2 of 11 radio-tagged eagles, both subadults, consisted largely (>20%) of the landfill; home-range size and percent of the home range that included the landfill were negatively correlated, suggesting that most eagles visited the landfill occasionally while a few spent most of their time there. We concluded that (1) the Vancouver landfill was not a major energy source for eagles, in part because their foraging is inefficient due to the large number of potential pirates; (2) most eagles apparently used the landfill primarily as a site for resting during inclement weather (the landfill is protected from the wind, is slightly warmer than surrounding areas due to decomposing refuse and the surrounding conifer trees, and is relatively free of human activity); and (3) a small population of largely subadult refuse specialists appeared to gain much or all of their energy from the landfill. *Received 14 December 2004, accepted 2 March 2006.*

Landfills can provide a constant and abundant food source for birds, potentially increasing reproductive success at nearby nesting colonies (Pons and Migot 1995, Tortosa et al. 2003) and allowing some regions to support otherwise unsustainable populations (Sibly and McCleery 1983). During the breeding season, landfills are particularly important for several species, including American Crow (*Corvus brachyrhynchos*, Stouffer and Caccamise 1991), Alpine [currently Yellow-billed] Chough (*Pyrrhocorax graculus*, Delestrade 1994), White Stork (*Ciconia ciconia*, Tortosa et al. 2003), Black Kite (*Milvus migrans*, Blanco 1997) and Common Raven (*Corvus corax*, Restani et al. 2001). Foraging at landfills, however, can lower avian survivorship and reproduction (Pierotti and Annett 1991, Smith and Carlile 1993, Annett and Pierotti 1999) due to poor food quality (Smith and Carlile 1993, Annett and Pierotti 1999), increased transmission of disease (Durrant and Beatson 1981, Monaghan et al. 1985, Ortiz and Smith 1994), ingestion of synthetics (Inigo Elias 1987), and contamination by toxins (Millsap et al. 2005). During the nonbreeding season, some populations of Bald Eagles (*Haliaeetus leucocephalus*) are highly mobile foragers, traveling thousands of km to congregate where food is abundant (Knight and Knight 1983, Knight and Skagen 1988, Restani et al. 2000). Because food availability during late winter is critical to eagle survivorship (Sherrod et al. 1976, Stalmaster and Gessaman 1984), the additional food available at landfills might contribute to increases in local eagle populations (Hancock 2003). Sherrod et al. (1976) and Jackson (1981) attributed a population increase of eagles to increased food supply at a landfill.

Understanding the population effects of landfills in British Columbia is important for several reasons. Moul and Gebauer (2002), Sullivan et al. (2002), and Vennesland (2004) suggested that landfills increased eagle carrying capacities, which, in turn, impacted waterbird populations. Increased eagle numbers

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in the Pacific Northwest (Dunwiddie and Kuntz 2001, Watson et al. 2002), purportedly due to anthropogenic food sources, has led some First Nation groups of British Columbia to request permission to harvest eagles. The Vancouver landfill manager is considering a number of bird-harassment techniques, including covering the active area with netting, to reduce bird numbers and the potential for aircraft-bird collisions at a nearby airport (P. Henderson pers. comm.). The potential consequence of such practices on eagle populations is unknown.

On the other hand, eagles have died from pentobarbital poisoning after eating euthanized animals that were improperly wrapped at landfills on Vancouver Island, Canada (three poisoned; Wilson et al. 1997), and at numerous locations in the United States (50 cases nationwide; Millsap et al. 2005). Millsap et al. (2005) reported reduced survival of "suburban" eagles compared with "rural" eagles, with 11% ($n = 18$) of mortality occurring at landfills. While no eagle mortality has been reported at the Vancouver landfill (Elliott et al. 1996, 1997), dozens of Glaucous-winged Gulls (*Larus glaucescens*) died in 1999 following ingestion of chocolate at this landfill.

Despite the abundance of literature concerning eagle foraging ecology and the large number of eagles that frequent landfills throughout North America (Stalmaster 1987, Gerrard and Bortolotti 1988, Buehler 2000), there are few published reports on the relevance of landfills to eagle foraging and population ecology. We initiated a study to determine (1) diet and time budgets of eagles visiting the Vancouver landfill; (2) whether food from the landfill provided a large energy source for local eagle populations; and (3) effects of eagle density, age, and weather on eagle behavior. Because eagles in the Pacific Northwest are primarily avivores in late winter (Watson et al. 1991, Hunt et al. 1992, Peterson et al. 2001), we suspected that eagles at the Vancouver landfill fed primarily on the gulls (>30,000) that regularly visit the site in mid-winter (Ward 1973). We expected that intraspecific pirating also would play an important role at the landfill, as it does along salmon streams (Stalmaster and Gessaman 1984, Hansen 1986, Knight and Skagen 1988).

METHODS

Study area.—The Vancouver landfill (49° 15′ N, 123° 10′ W), located near Vancouver, British Columbia, Canada, is a 10-ha disposal site for urban and commercial waste. Surrounding the landfill are agricultural lands where eagles often hunt or scavenge ducks foraging on winter cover crops. Boundary Bay—where eagles often hunt and scavenge wintering waterfowl numbering in the hundreds of thousands—is 5 km south of the landfill. During 1994–1998, there were five major eagle roosts within a 5-km radius of the landfill (Peterson et al. 2001), including one at Deas Island (49° 18′ N, 123° 10′ W) and South Arm (49° 18′ N, 123° 108′ W).

The landfill included an active refuse-deposition area (~1 ha), where most eagle foraging occurred. Many additional eagles perched in the trees and on fence posts surrounding the landfill. The location of the active area changed yearly. Although eagles at the landfill were continually surrounded by loud machines, the machines did not deter the birds, as they regularly perched on active machinery or grabbed food as it was being dumped, compacted, or moved. By contrast, eagles in surrounding areas were often harassed by dogs, photographers, eagle-watchers, and automobiles, and there have been a number of recent instances where eagles have been shot in Greater Vancouver. For example, during 1998–2001, three large roost sites—including Deas Island and South Arm—are believed to have been abandoned (the birds moving elsewhere) due to nearby housing developments.

Observations.—To determine diets, time budgets, and foraging behaviors, we visited the Vancouver landfill at least once per week from 11 January to 18 April 1994 (total observation = 132 hr), 25 January to 1 March 1995 (48 hr), 13 February to 28 March 1996 (68 hr), and 10 November 2001 to 28 April 2002 (224 hr). Observations took place between 06:00 and 20:00 PST in 4-hr, randomly chosen blocks. All observations were made by at least two observers inside a vehicle approximately 50 m from the active area. Due to topography of the active area, we were unable to make observations from elsewhere. Eagles were habituated to vehicles and heavy machinery, which were always present and often <50 m from eagles, so it seemed unlikely that we influenced eagle behavior. Because virtually all foraging occurred within the active area (>99%), and because we could monitor most of the entire landfill from our vantage point atop the landfill, we concluded that our observations included all foraging events.

Once each hour, we drove around the rim of the landfill, counted adult and subadult eagles, and classified eagle behaviors as resting, bathing, preening, pirating, eating, scavenging, drinking, or hunting. We classified all eagles <5 years old as subadults according to the methods outlined in McCollough (1989). We classified eagle behavior as follows: pirating (chasing or harassing another bird carrying or eating food), scavenging (picking through the garbage in the landfill active area), and foraging (carrying food, pirating, scavenging, or hunting). We classified the number of food items obtained per eagle foraging attempt as "foraging efficiency." During 1994–1998, we also visited two roost sites (Deas Island and South Arm) beginning an hour prior to sunset twice a week and recorded direction of arrival to determine whether the eagles at the landfill were using these roost sites.

We recorded wind speed, precipitation, temperature, and percent cloud cover at the active site at the beginning and end of each observation period. For analysis, beginning and ending values were averaged. Detection probabilities for adult versus subadult eagles can vary, especially when the birds are perched (Anthony et al. 1999). However, the proportion of subadults seen flying and foraging at the landfill was similar to the proportion seen roosting in the surrounding trees (KHE unpubl. data); thus, we concluded that we counted all eagles present (Hancock 1964, Anthony et al. 1999). We recorded the direction of arrival or departure of all incoming or outgoing eagles.

Energy consumption.—Following the protocol set out by Dykstra et al. (1998), Warnke et al. (2002), and Gill and Elliott (2003), we identified any item an eagle attempted to eat during the observation period and estimated its size relative to the eagle's talons or mandibles. At the beginning of each field season, we spent 10 hr practicing food-item identification. Based on 104 items retrieved later, we obtained accuracies of >95% for classifying type and size and 80% for estimating food mass based on size estimates. We assumed, therefore, that our mass estimates were accurate to within 20%. We estimated the mass and caloric value of each food item based on its size by using a sample of food items collected at the landfill or from a local grocery store. We classified each food item as red meat waste (mammalian origin, including bones and suet), chicken, gull, rat, garbage, or fish. To estimate post-assimilation energetic efficiencies, we used the mass-specific energetic and percent edible values provided in Stalmaster and Gessaman (1982) for captive eagles feeding on mammalian meat (black-tailed jackrabbit, *Lepus californicus*), birds (Mallard, *Anas platyrhynchos*), and fish (chum salmon, *Oncorhynchus keta*). We necessarily assumed that bone and suet had mass-specific post-assimilation energetic values identical to jackrabbit. Thus, we (1) estimated size and categorized food items; (2) used regressions on a sample of items we collected and weighed to develop an item-specific relationship between size and mass; (3) used the regression between size and mass on a subsample of measured items to estimate the mass of each food item observed; (4) used mass-specific caloric values from the literature to estimate actual caloric values of each food item observed; and (5) estimated digestive efficiency from Stalmaster and Gessaman's (1982) post-assimilation energetic efficiencies to determine actual energy absorbed.

Since the main factors influencing energy intake and number of eagles present were time of day and date, respectively (see Results), and because both of these relationships were clearly nonlinear, we used Akaike's Information Criterion (AIC_c) to determine what higher-order polynomial best described the relationships between energy intake versus time of day, and number of eagles present versus date (Burnham and Anderson 1998:66–67). In both cases, quadratic polynomials provided the best fit (energy intake: $\Delta AIC_c = 8.5$; number of birds: $\Delta AIC_c = 26.1$, compared to the null model). Thus, we used the relationship between energy intake and time of day observed during our random observation periods to estimate the total number of food items taken for each day:

$$\sum_i \alpha + \beta T_i + \gamma T^2_i,$$

where α, β and γ are the coefficients for the quadratic regression of number of prey items eaten per hour against number of hours after sunrise (T_i). The summation was taken over all hours between 0.5 hr before sunrise and 0.5 hr after sunset. Energy intake per day is the product of average energetic value of food items, *n*, and the number of food items per day, assuming energy content of food items does not change with time of day or date:

$$\sum_i n(\alpha + \beta T_i + \gamma T^2_i).$$

Finally, energy intake per day is divided by the predicted number of eagles to determine the energy intake per eagle per day:

$$\sum_{i,j} \frac{n(\alpha + \beta T_i + \gamma T^2_i)}{a + bD_j + cD^2_j},$$

where *a*, *b* and *c* are the coefficients for the quadratic regression of the number of eagles present against date (D_j). The summation was taken over all dates between 1 February and 31 March. An alternative formula, which averaged energy intake for each observation period over the entire season, provided almost identical results (KHE unpubl. data).

To estimate the population increase resulting from energy obtained at the landfill, we used Stalmaster's (1983) model, which converts salmon carcass availability into "Eagle Use Days." We modified the "consumable salmon biomass" section of the model to represent the average energy intake of eagles at the landfill (207 ± 62 kJ/day; see Results). We set the flight time to 0.084 hr/day (0.7% of a 12-hr day; see Results) and human disturbance to 0 hr (human disturbance at the landfill was minimal); otherwise, we used default values reported in Stalmaster (1983). The 20% error estimate associated with food energy estimates and the error estimate (SD) associated with the quadratic regression coefficients were propagated through the formula following Stalmaster (1983). This uncertainty was then increased by 19% to account for error within the model itself (Stalmaster 1983).

Radio telemetry.—In the agricultural fields surrounding the landfill, we radio-tagged nine eagles (four adults, five subadults) during 22–31 January 1997 and three subadult eagles on 18 January 1998. We used 172 mHz backpack transmitters weighing 90 g (Advanced Telemetry Systems, Isanti, Minnesota). Half-inch Teflon Ribbon (Bally Ribbon Mills, Bally, Pennsylvania) was used to attach transmitters in the backpack "X" configuration, as described by Buehler et al. (1995). Birds were caught using floating fish snares or padded leg-hold traps. Birds were tracked for 0–17 days over the next 3 months. Only verified (triangulated) locations were included in the analysis. To reduce bias, we only included the 11 individuals for which we had >15 samples. The fixed kernel density estimator (set at 95%), using least-squares cross validation, was calculated using the ArcView 3.2 Animal Movement Analysis extension (Hooge 2005) for individual birds. Fixed kernel calculates utilization distributions using a probabilistic model and infers the relative amount of time the animal spends in any one place. We calculated home-range size and the percent of the home range consisting of the landfill.

Statistical analysis.—For each behavior (resting, bathing, preening, pirating, eating, scavenging, drinking, and hunting), we constructed a linear model in which hours after sunrise, date, weather (cloud cover, precipitation, wind, and temperature), and number of eagles present were the independent variables. We also constructed linear models—with number of eagles, percent of eagles foraging or pirating, and foraging efficiency as dependent variables—and weather (cloud cover, precipitation, wind, and temperature), date, hours after sunrise, number of eagles, number of pirating events, and percent of eagles foraging as independent variables. We inserted quadratic terms into the models to account for the dependence of eagle numbers on date and foraging on time of day, as described above. For each model we used a positive stepwise method to remove all nonsignificant factors (at $P < 0.05$). We report the R^2 values for the model that included only significant factors. We used contingency tables with Yates' correction for continuity to compare behaviors of subadults and adults (Zar 1999). We used Rayleigh's Test to determine whether the directions of birds coming in to roosts coincided

TABLE 1. Foods consumed by Bald Eagles at the Vancouver landfill, British Columbia, Canada, during 1993–1996 and 2001–2002. Eagles consumed primarily red meat waste (mammalian origin) and bones.

Food item	No. consumed	Percent of total diet	Wet mass (g)[a]	Energetic value (kJ)[a,b]
Red meat waste	194	30.7	320 (35)	1,160 (130)
Bones	142	22.4	450 (35)	1,625 (125)
Garbage[c]	42	6.6	210 (50)	0
Fat/suet	26	4.1	340 (70)	1,230 (250)
Glaucous-winged Gull[d]	14	2.2	980 (90)	5,505 (500)
Fish	3	0.4	310 (80)	920 (240)
Rat	2	0.3	245 (80)	890 (290)
Chicken	1	0.2	480	2,700
Unknown	204	32.3		

[a] Mean value (SE).

[b] Based on the mean estimated mass, using the percent edibility from Stalmaster and Gessaman (1982) and mass-specific caloric information provided by the appropriate food labels from nearby grocery stores or the literature.

[c] Includes inedible items, largely paper.

[d] Includes 10 scavenged and 4 killed gulls.

with directions from the landfill (Batschelet 1981). We performed all tests in STATISTICA (StatSoft, Inc. 2004). We tested for normality (Kolmogrov-Smirnov) and homogeneity of variance (Levine's test) before using parametric statistics, and we used arcsine transformations prior to doing statistical tests on percentages. Our P-values include Bonferroni adjustments for multiple comparisons, as calculated by STATISTICA. If analysis of covariance provided no significant variation between years, data from separate years were pooled. Results were considered significant if $P < 0.05$. Results are presented as means ± SE.

RESULTS

Diet and energy intake.—Household food refuse, particularly red meat waste and bones, made up 95% of known food items of Bald Eagles foraging at the landfill (Table 1). Although some meat was identifiable (e.g., sausage or hamburger), most was unidentifiable and clearly putrid or decomposing. Eagles also consumed garbage, including paper towels and plastic bags. Glaucous-winged Gulls (10 scavenged, 4 captured live) composed only 2.2% of the diet. Average energy intake per eagle was 207 ± 62 kJ/day, which was 10 ± 3% of the required daily energy intake. The number of "Eagle Use Days" (1,300 ± 400) at the landfill during the winter was equivalent to 17 ± 5 eagles over the peak period of use from February–March.

Time budgets and behavior.—Eagles at the landfill spent most (91.0%) of their time resting. Resting occurred primarily later in the day and when more eagles were present. Resting was linearly related ($R^2 = 0.21$) to number of hours after sunrise ($t_{185} = -4.4$, $P < 0.001$) and wind ($t_{186} = 4.0$, $P = 0.004$). Percent time bathing (0.06%), drinking (2.6%), eating (1.2%), flying (0.7%), hunting (0.3%), pirating (1.8%), preening (0.6%) and scavenging (2.3%) were not explained by environmental variables.

Peak numbers at both the landfill and nearby roosts occurred in late winter (Fig. 1), after eagle numbers had peaked at local salmon spawning streams (Dunwiddie and Kuntz 2001). The highest count was 453 on 26 February 2001 (Fig. 1). The percentage of adults present at both the landfill and nearby roosts declined with date at similar rates (Fig. 1). The percentage of eagles foraging declined as the number of eagles present increased and when precipitation fell (Table 2), and was greatest during the first 3 hr after sunrise (Fig. 2). Foraging efficiency increased as wind speed increased, and it declined with date, number of eagles pirating, number of eagles present, and when precipitation fell (Table 2). Overall, 60% of food items obtained were later pirated; 84% of theft attempts were directed against other eagles; and 16% were directed against gulls. The percentage of eagles pirating increased as the percentage of eagles foraging increased, and decreased with the number of eagles present (Table 2). The likelihood of a food item being pirated increased with size of the food item ($R^2 = 0.45$, $P < 0.001$).

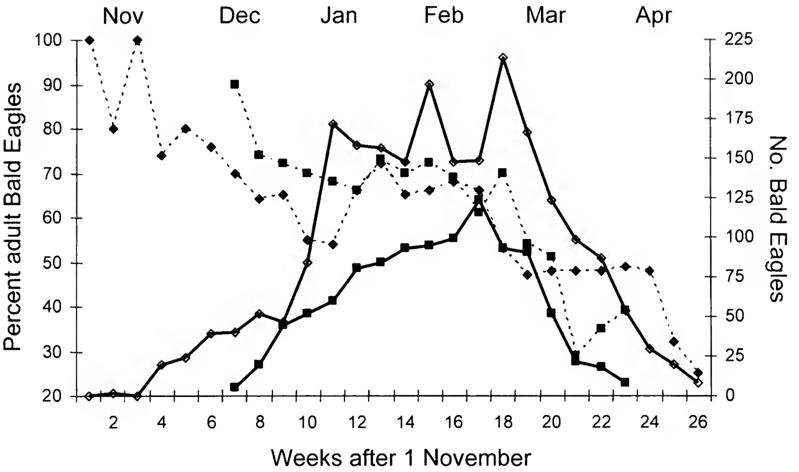

FIG. 1. Bald Eagle numbers (solid lines) and the percentage of adult (as opposed to subadult) eagles (hatched lines) present at the Vancouver, British Columbia, Canada, landfill (diamonds) and at two nearby roost sites (squares) during the weeks after 1 November. Eagle numbers are weekly averages of daily peak numbers, and percentages of adult eagles are weekly averages. Values were averaged over 1993–1996 and 2001–2002 (landfill) and 1993–1996 (roosts) winters. Roosts were inactive in 2001–2002.

Subadults spent more time pirating, scavenging, flying, and bathing, whereas adults spent more time hunting and resting (Table 3); however, foraging efficiency and pirating success were similar between adults and subadults (Table 3).

Eagles arriving to roost at the South Arm and Deas Island sites came from significantly different directions than that of the landfill ($Z = 14.5$, $P < 0.001$). Eagles arrived at the landfill primarily from adjacent agricultural fields and not from the South Arm and Deas Island roosts ($Z = 18.6$, $P < 0.001$).

Radio telemetry.—Six of the 11 radio-tagged eagles had home ranges that included the landfill (Table 4, Fig. 3). There was no relationship between number of points used for analysis and home-range size. The two in-

TABLE 2. Number of eagles present at the Vancouver landfill, British Columbia, Canada, 1993–2002. Eagle numbers increased with increasing wind, precipitation, and cloud cover. The percentage of eagles foraging decreased with precipitation and number of eagles present. The percentage of eagles pirating decreased with number of eagles but increased with number of eagles foraging. Foraging efficiency increased with wind and decreased with precipitation, date, number of eagles present, and number of eagles pirating.

	No. eagles		Eagles foraging (%)		Eagles pirating (%)		Foraging efficiency[a]	
Effect	t_{187}	P	T_{186}	P	t_{187}	P	t_{186}	P
Wind	4.2	<0.001		NS[b]		NS	2.6	0.012
Precipitation	4.1	<0.001	−2.1	0.010		NS	−2.4	0.019
Cloud cover	7.5	<0.001		NS		NS		NS
Date		—[c]		NS		NS	−3.1	0.002
Temperature		NS		NS		NS		NS
Hour after sunrise		NS		—[d]		NS		NS
No. eagles present		—	−2.7	0.007	−2.7	0.008	−2.4	0.02
Eagles foraging (%)		NS		—	3.0	<0.001		NS
No. eagles pirating		NS		NS	—		−9.9	<0.001
R[e]		0.46		0.48		0.08		0.53

[a] Number of food items taken per foraging attempt.
[b] Not significant ($P > 0.05$).
[c] The linear model for number of eagles fitted to a quadratic term to account for the effect of date.
[d] The linear model for percentage of eagles foraging fitted to a quadratic term to account for the effect of hours after sunrise.
[e] Refers to the total linear model once nonsignificant factors have been removed (positive stepwise).

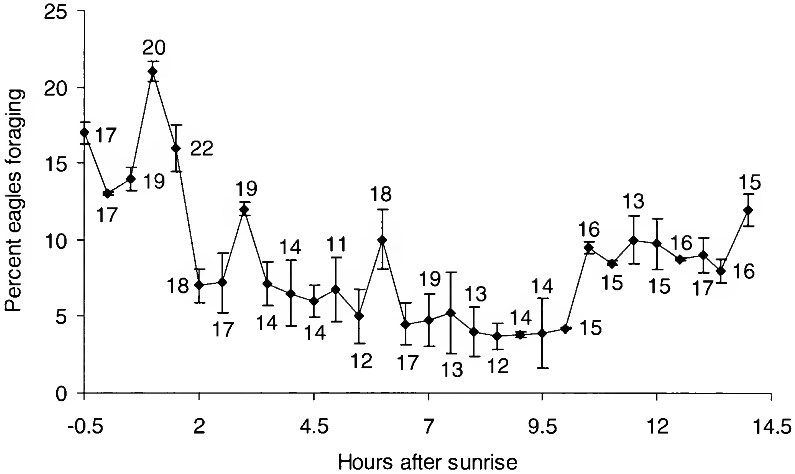

FIG. 2. Percent of eagles foraging in relation to hours after sunrise at the Vancouver, British Columbia, Canada, landfill during the winters of 1993–1996 and 2001–2002. Peak foraging occurred in early and late hours of the day. Based on these data, the quadratic regression for percent of eagles foraging = 0.18(time of day)^2 −2.8(time of day) ± 16; $R^2 = 0.67$. Error bars represent SE; sample sizes appear above, below, or to the right of data points.

dividuals whose home ranges largely consisted of the Vancouver landfill (e.g., >10% of their home range was the Vancouver landfill) had the smallest home ranges, and home-range size was negatively correlated with the percentage of the home range that encompassed the landfill ($t_5 = -3.05$, $P = 0.04$, $r^2 = 0.70$).

TABLE 3. Percent time adult and subadult Bald Eagles spent engaged in various behaviors at the Vancouver landfill, British Columbia, Canada, 1993–2002. Adults spent more time resting and hunting than subadults, whereas subadults spent more time scavenging, pirating, flying, and bathing. Foraging efficiency, pirating success, and percent time spent drinking and preening were equivalent between the two groups.

Behavior	Adult	Subadult	χ^2_1	P
Resting	93.1	88.2	3.7	0.048
Drinking	2.4	2.7		NS[a]
Scavenging	1.0	5.4	22.4	0.001
Pirating	0.5	4.9	33.7	0.001
Preening	0.6	0.6		NS
Flying	0.2	1.5	9.2	0.001
Hunting	0.8	0.1	5.5	0.016
Bathing	0.02	0.1	6.2	0.014
Foraging efficiency[b]	0.31	0.33		NS
Pirating success[c]	0.48	0.49		NS

[a] Not significant ($P > 0.05$).

[b] Number of food items taken per foraging attempt.

[c] Percentage of pirating attempts that were successful.

DISCUSSION

Contrary to initial expectations, the Vancouver landfill accounted for only 10 ± 3% of the energy intake of the eagles that frequent the landfill. Furthermore, the actual intake was likely <10% because we assumed liberal values for major food items, such as bone and rancid foods, and the eagles wasted considerable amounts of food that we could not quantify. Eagle behavior was similar to that of Herring Gulls (*Larus argentatus*), which use landfills primarily for social interaction and loafing, especially when higher-quality food is available elsewhere (Belant et al. 1993). Nearby waterfowl concentrations probably represented a higher-quality food base (Peterson et

TABLE 4. Home-range sizes of eagles radio-tagged near the Vancouver landfill, British Columbia, Canada, decreased during winter 1997 and 1998 as the landfill portion of their home range increased.

Bird	Year	Age	Area in landfill (%)	Home range (km^2)
373	1997	Subadult	1.7	20.4
241	1997	Subadult	1.5	27.8
190	1997	Adult	0.9	37.3
210	1998	Subadult	3.4	14.2
072	1998	Subadult	20.4	2.5
062	1998	Subadult	50.6	1.5

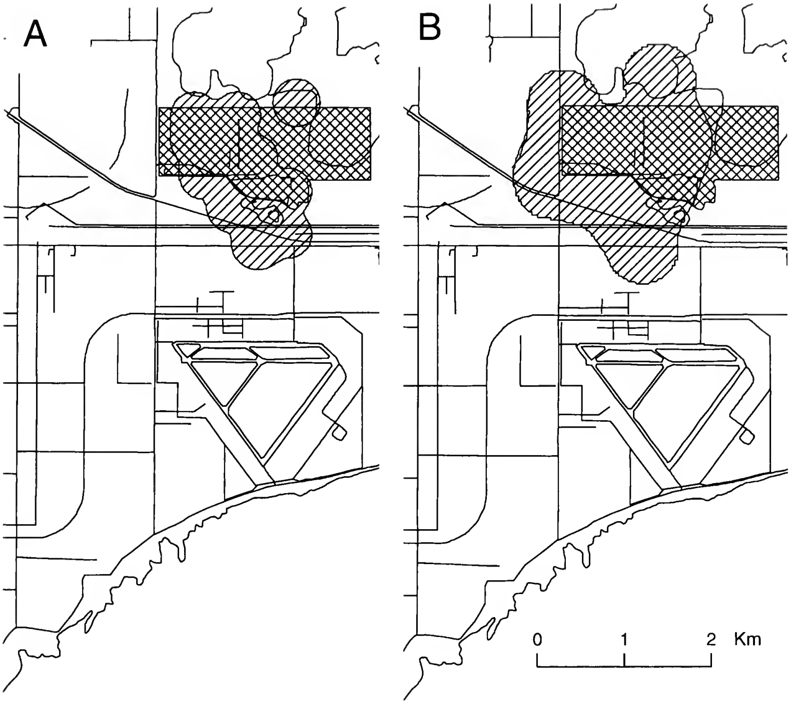

FIG. 3. Home ranges of two (A, B) "refuse specialist" Bald Eagles (>20% of their home ranges comprised the Vancouver landfill) radiotagged near the landfill in Vancouver, British Columbia, Canada, during the winters of 1997 and 1998. Forward slashes (///) represent eagle home ranges; crosshatching represents the Vancouver landfill.

al. 2001), and most eagles may have foraged on waterfowl. Consistent with this hypothesis, resting and overall numbers of eagles peaked during periods of inclement weather because the landfill is protected from the wind, is slightly warmer due to decomposing refuse and surrounding conifer trees, and is relatively free of human disturbance—all of which are known to reduce the energetic costs associated with resting (Stalmaster and Newman 1979, Keister et al. 1985). The possibility of feeding at the landfill was likely an added bonus.

It is improbable that the landfill contributed significantly to an increased eagle carrying capacity in the region, as the observed energy intake only accounted for an additional 17 ± 5 eagles during peak eagle use. This is a very small number compared to the 500–1,000 eagles that use the surrounding area in late winter, and it does not account for the 30-fold population increase that has occurred over the last 30 years. Percent of eagles foraging declined with a decrease in the number of eagles present, suggesting that the number of foragers stayed relatively constant and the remainder only visited to rest. Thus, some eagles (the refuse specialists) may have foraged primarily at the landfill and obtained much of their energy needs there. Furthermore, the standard deviation for average energy intake (264 kJ/day) was greater than the average intake rate (207 kJ/day) itself, indicating wide variation among individuals.

Consistent with the existence of refuse specialists, 2 of 11 (18%) radio-tagged eagles had a fixed kernel home range that mostly (>20%) included the landfill, whereas another 4 visited the landfill only occasionally (Table 4). Visual inspection of the home ranges of the two refuse specialists suggests that they rarely left the landfill; most of the points outside the landfill appeared to be in adjacent conifer trees, which are used for resting (Fig. 3). The refuse specialist estimate (18%) is quite close to our estimate for the proportion of the local population that was supported by energy intake from the landfill (10 ± 2%). It appears that younger eagles were the refuse specialists, because they spent more of their time foraging and older eagles spent more time resting at the landfill—possibly because younger eagles are less efficient hunters than the adults (Stalmaster and Gessaman 1984, Brown 1993, Bennetts and McClelland 1997). A similar study at a nearby salmon stream in late winter showed a strong relationship between pirating success and age (Stalmaster and Gessaman 1984), and, at the Vancouver landfill, subadults pirated more than adults; this may reflect a change in dominance structure associated with the predictability of anthropogenic food sources (e.g., Restani et al. 2001). Moreover, home ranges of refuse specialists in a wide variety of taxa are much smaller than the average home range size, and reduced home range size is often associated with a change in social structure due to increased density at landfills (e.g., Blanchard and Knight 1991, Delestrade 1994, Gilchrist and Otali 2002).

Pirating was common at the Vancouver landfill, which may partially explain why few eagles forage there. Foraging efficiency and the percent of birds foraging declined as the number of birds present and pirating increased. Although piracy is also common at waterfowl carcasses (Peterson et al. 2001) and salmon streams (Stalmaster and Gessman 1984), it may be that the higher quality of those food types makes pirating them more worthwhile energetically. Eagles at the landfill pirated primarily conspecifics; thus, although both gulls and eagles competed for the same resource (human refuse), there appeared to be few interactions between them.

At both the landfill and nearby roosts, the timing of peak eagle numbers and the percentage of adults present were similar, supporting our assumption (based on radiotelemetry) that individuals regularly moved between these sites (this study, Servheen and English 1979, Hunt et al. 1992). The percentage of subadults increased over the winter at both locations, not only because subadults learned about food concentrations from adults (Knight and Knight 1983, Bennetts and McClelland 1997, Restani et al. 2000), but also because many breeders returned to their territories in late fall (Stalmaster and Kaiser 1997).

Eagles spent most of their time resting (91%). At the landfill, they rested more than they did at the Columbia River estuary (54%; Watson et al. 1991), and they spent less time flying (0.7% versus 6%). Overall, time spent flying was similar to that reported on the Nooksack River (1.0%; Stalmaster and Gessaman 1984). In previous studies, eagles (Sherrod et al. 1976) and gulls (Sibly and McCleery 1983, Coulson et al. 1987) at several landfills foraged whenever the landfills were active, with peak foraging occurring when the landfill machinery activities stopped. In contrast, eagles at the Vancouver landfill—where food was available almost continuously because refuse dumping started every day before sunrise (06:30) and did not end until after sunset (18:30)—foraged primarily during early morning and late afternoon (Fig. 2). This reflects the typical diurnal feeding patterns of eagles (Watson et al. 1991; Elliott et al. 2003, 2005), as well as the short day length during Vancouver winters.

ACKNOWLEDGMENTS

We thank P. Henderson and the Greater Vancouver Regional District for permission to enter the landfill. M. Porter provided interesting anecdotal information. L. L. Jordison helped with some of the surveys. A. Fabro provided us with copies of some of the more obscure literature. J. M. Touchton and the Smithsonian Tropical Research Institute provided computer support. R. W. Butler, W. G. Hunt, A. R. Harmata, J. W. Watson, and an anonymous reviewer provided valuable comments on an earlier draft of this manuscript.

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The Wilson Journal of Ornithology 118(3):391–398, 2006

TERRITORY SELECTION BY UPLAND RED-WINGED BLACKBIRDS IN EXPERIMENTAL RESTORATION PLOTS

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ABSTRACT.—We examined territory selection of Red-winged Blackbirds (*Agelaius phoeniceus*) in experimental treatments with varied groundcovers and densities of planted and naturally occurring oaks (*Quercus* spp.) used by blackbirds for perching. We also compared vegetation parameters between blackbird territories and unused (i.e., unoccupied by Red-winged Blackbirds) areas. Although perch densities were greater in blackbird territories in unplanted controls and oak-planted treatments without redtop grass (*Agrostis gigantea*) than they were in unused areas, the low densities of perches in territories planted with redtop grass indicate that perch density is not limiting above some lower threshold. Territories, particularly in treatments with no redtop, tended to have greater mean grass cover and taller grass heights than unused areas. Our results are consistent with other studies in finding that Red-winged Blackbirds prefer areas having tall vegetation and dense grass. *Received 14 July 2005, accepted 21 February 2006.*

A large body of observational studies has documented relationships between avian abundance, or territory use, and vegetation parameters. Examples include studies comparing differences among songbird territories with respect to vegetation height or litter depth (Wiens 1969) and grass or shrub cover (Rotenberry and Wiens 1980), and those that relate avian abundance to vegetation density (Orians and Wittenberger 1991) or grass (Scott et al. 2002). However, important relationships between vegetation and habitat use can be obscured if the variation among study sites (or plots) is minimal (Orians and Wittenberger 1991, Pribil and Picman 1997). One way to elucidate habitat variation and distinguish factors important in habitat selection is by comparing sites that differ explicitly in terms of vegetation management. For example, Shochat et al. (2005), Wood et al. (2004), and Murkin et al. (1997) evaluated avian responses among plots that varied with respect to management regime, and were able to make clear inferences that may have been obscured had they studied only unmanaged habitats.

Even where variation among plots is made explicit, however, the influences of vegetative factors on avian settlement patterns may be masked if measurements are made at inappropriate scales (Orians and Wittenberger 1991, Pribil and Picman 1997). For example, Orians and Wittenberger (1991) found that Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) settle according to food supplies at the scale of an entire marsh, a relationship that was not apparent at the territory scale. Similarly, Burhans (1997) found that some factors explaining brood parasitism at the nest-site scale were relevant only when considered at the larger scale of habitat.

We investigated the role of vegetation structure in the selection of breeding territories by Red-winged Blackbirds (*Agelaius phoeniceus*) in two experimentally manipulated restoration sites of floodplain oak (*Quercus* spp.) near the Missouri River. Numerous researchers have investigated habitat selection by Red-winged Blackbirds (Albers 1978, Joyner 1978, Pribill and Picman 1997, Turner and McCarthy 1998), and some have examined responses of Red-winged Blackbirds and other species within plots characterized by differing management regimes (Herkert 1994, McCoy et al. 2001, LaPointe et al. 2003); however, our study is the only one we know of in which more than one factor varied (i.e., perch availability and grass cover) among adjoining treatment plots within the same sites. These plots varied with respect to densities of planted trees, which blackbirds used as perches, and the presence or absence of a planted cover crop. Typically, managed plots in other songbird studies have been geographically sepa-

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rated (Herkert 1994, Swengel 1996, McCoy et al. 2001); however, our plots shared common boundaries to allow comparisons of habitat selection without the confounding effects of between-site variation.

We specifically wished to determine (1) how the availability of perches and vegetation determines Red-winged Blackbird territory use and density at the treatment scale, and (2) how within-treatment vegetation composition and structure in territories would compare with unused (i.e., unoccupied by Red-winged Blackbirds) areas. We were particularly interested in determining the importance of grass cover and density, because a dense, short-stature cover crop of grass (redtop, *Agrostis gigantea*) planted at our sites had suppressed invading vegetation but was unsuitable for nesting, whereas the common invasive—Johnsongrass (*Sorghum halepense*), which was also present—potentially provided a tall nesting substrate and cover. Because blackbirds in upland settings prefer dense, tall cover (Albers 1978, Bollinger 1995), we predicted that density of blackbird territories would be greater in treatments not planted with redtop. Within treatments, we predicted that blackbird territories would be characterized by denser, taller cover than unused areas. Based on previous studies establishing the importance of perches (Joyner 1978, Payne et al. 1998), we predicted that densities of Red-winged Blackbird territories would be greater in treatments planted with oaks, and that territories would have perches located at greater heights and at greater densities than unused areas.

METHODS

Study site.—Our research was conducted in central Missouri at two sites located within the Missouri River Floodplain. Plowboy Bend Conservation Area (38° 48′ 5″ N, 92° 24′ 17″ W), a landscape dominated by row-crop agriculture, is located west of the Missouri River's main channel within a levee-protected floodplain. Smoky Waters Conservation Area (38° 35′ 9″ N, 91° 58′ 3″ W) is located 72 km southeast of Plowboy Bend, between the Missouri River's main channel and the Osage River. Smoky Waters' floodplain has not been protected since a levee was breached there in the 1993 and 1995 floods; thus, it is subject to occasional flooding.

Both study sites encompassed three 16.2-ha, adjacent experimental treatments (hereafter, "blocks") that differed with respect to vegetation treatments. The blocks—formerly row-cropped—were established in 1999 for an ongoing research project to evaluate the restoration of hard mast (oak acorn; Dey et al. 2003). Oaks were planted at a density of 119 trees/ha (Dey et al. 2003). During our study, half of the planted oaks were >1.5 m high and were often used as perches by Red-winged Blackbirds (MAF pers. obs.). Each site had three treatment blocks with varying densities of planted and natural perches. (1) "Redtop" blocks, seeded with a uniform cover of redtop grass, were planted with saplings of swamp white (*Quercus bicolor*) and pin (*Q. palustris*) oaks distributed in planting units that varied in terms of planting methods but had a uniform ground cover of redtop grass (for details, see Dey et al. 2003). The redtop grass produced a low, dense ground cover that largely suppressed invasion by other herbaceous and woody vegetation that otherwise may have been used as perches or nest sites by Red-winged Blackbirds; thus, redtop blocks contained some planted oak perches but few or no natural perches. (2) "No redtop" blocks contained the same configuration of oak plantings described above for redtop blocks, but they were not seeded with a ground cover; therefore, over time they contained taller, denser shrubs, trees, and herbaceous vegetation and more "natural" unplanted perches than redtop blocks. (3) "Control" blocks contained only natural perches, such as invading forbs and shrubs, and no oak plantings or any of the vegetation treatments listed above.

Delineation of breeding territories.—We identified breeding territories from March to May in 2001 and 2002 by monitoring male Red-winged Blackbirds exhibiting mating behaviors, such as the "song spread" (Yasukawa and Searcy 1995) and territory defense. To delineate territories, we conducted consecutive flushing (Wiens 1969), a technique in which males are approached and followed until they alight on the perches that define their territory. Territories were delineated by identifying and flagging at least four perches used consecutively by each male (mean number of perches flagged/territory = 7.12 ± 1.97 SD).

Vegetation measurements.—Once a breeding territory was completely flagged, we recorded the location, species, and height (m) for each perch. We established two 1-m-wide belt transects in each territory to estimate density of potential perches (no. stems >1.5 m tall/m^2) and determined average maximum stem height (m). To establish the first transect, the center of the territory was visually located and staked; then a random azimuth was determined to establish the direction of the transect across the territory. The second transect location was established perpendicular to the first. Using a 1-m stick held horizontally at 1.5 m above ground, we walked the territory end-to-end along each transect, recording the number of stem contacts and the maximum vegetation height (m) at 1-m intervals. Two vertical density-board measurements were taken at random locations along each transect, resulting in four individual measurements of vertical vegetation structure for each breeding territory. The proportion of vertical vegetation was estimated using a 9-increment density board (2.25 m tall × 0.25 m wide). At each 0.25-m increment, we estimated the proportion of living and dead vegetation from a distance of 15 m. We estimated the proportion in each increment for woody, forb (herbaceous), and grass vegetation and combined them to generate an estimate of mean total proportion.

We randomly located unused plots (unoccupied by Red-winged Blackbirds) by using a 100-m interval grid of UTM (Universal Transmercator) coordinates placed over the restoration sites where there were no active territories. Sampling of vegetation structure was identical to that conducted within blackbird territories, with the exception that belt-transect length within a given site was based on the average belt-transect length of all breeding territories found at the site.

Statistical analyses.—For each year, we calculated territory density for each block type (redtop, no redtop, control) by summing the numbers of territories found in each block type and dividing by 16.2 ha. If a territory straddled more than one block type, we placed it in the block type in which the majority of its area occurred.

We averaged vegetation variables for the four samples taken within each blackbird territory. For vertical vegetation measurements, the mean was calculated from all of the 0.25-m increments for each vegetation type of interest (woody, forb, grass, and total vertical vegetation). Of the vertical vegetation measurements, we included only mean total vertical cover, mean vertical grass cover, and mean grass height, which was defined as the last-recorded increment having grass cover on the vertical density board. We reasoned that mean total vertical cover was important if blackbirds were assessing territories based on cover without regard to vegetation type. We examined grass cover and height because of the apparent differences in grass cover between redtop blocks and the other block types.

We also used the vertical vegetation measurements to create a variable called "threshold nest-cover height," defined as the lowest height at which mean total vertical cover (based on the density board samples) was ≥60%. The latter value was based upon a 2001 sample of vegetation measured (using the same vertical density board methodology described above) at 99 Red-winged Blackbird nests. At the 99 nests, we determined that the mean total vertical cover at nest height (viewed 15 m from the board) was 60%; therefore, we assumed that blackbirds select nest sites with at least 60% total vertical cover. Typically, total vertical cover approached 100% near the ground, but decreased with distance above ground; thus, a high value of threshold nest-cover height (i.e., >60%) usually indicated denser cover below the threshold height, but less cover above. High values of threshold nest-cover height do not indicate that vertical cover was denser; rather, they indicate that the vertical height at which cover equaled or exceeded 60% was greater.

We used a general linear model (PROC MIXED; SAS Institute, Inc. 2003) to test for differences in territory density among block types. We nested block within site as a random effect to account for differences in site, and included "year" in the model to account for additional variation. We used the likelihood ratio test to test the overall model against a null model that included only the intercept. If the overall model was significant, we used the LSMEANS statement to examine whether territory densities varied among the three block types (control, no redtop, redtop); we considered differences at $P \leq 0.05$ to be significant.

We analyzed vegetation differences among block types, by site, using PROC MIXED models as above, again using likelihood ratio tests to compare models against a null model. Because there were a large number of vegetation variables, for which one or several tests could be significant by chance, we used the sequential Bonferroni method to interpret overall model significance (Rice 1989). Although the sequential Bonferroni test has been criticized as overly conservative in circumstances where numerous individual tests show moderately significant results (Moran 2003), in this circumstance we feel that it was a suitable compromise between having no control for type I error and the simple Bonferroni test, which is even more conservative (Rice 1989). If the overall model was significant, we used the LSMEANS statement to determine whether territory area and vegetation variables varied among the three block types (control, no redtop, redtop), by site; within each model, we considered differences at adjusted $P \leq 0.05$ to be significant.

We also compared parameters of vegetation structure between areas occupied ("territories") and unoccupied ("unused" plots) by Red-winged Blackbirds to describe local vegetation differences affecting blackbird habitat selection within blocks. Because flooding events in 2001 prevented us from sampling unused plots at both sites, only 2002 field data were used for this analysis, and we removed territory and unused samples entirely if any data values were missing. We used a general linear model (PROC MIXED; SAS Institute, Inc. 2003) with an LSMEANS statement to calculate means and standard errors for each variable of interest. We determined that there were differences among territories and unused plots if likelihood ratio tests indicated overall model significance, based on sequential Bonferroni adjustments for the six vegetation variables analyzed. If the overall model was significant, we evaluated multiple comparisons among different combinations of block, territory, and unused plots (15 comparisons per model) with sequential Bonferroni tests to control for type I error.

RESULTS

We analyzed 81 Red-winged Blackbird breeding territories across both sites and years. Mean breeding territory area in 2001 was 1,667 ± 195 m^2 ($n = 19$), 1,897 ± 221 m^2 ($n = 17$), and 2,310 ± 464 m^2 ($n = 10$) in redtop, no redtop, and control blocks, respectively, and in 2002 it was 1,648 ± 173 m^2 ($n = 14$), 1,808 ± 269 m^2 ($n = 17$), and 771 ± 83 m^2 ($n = 4$). We found no differences in territory area by block type (likelihood ratio test: $\chi^2 = 2.3$, df = 3, $P = 0.51$). In 2001, mean territory density across both sites was 0.71 ± 0.74, 0.67 ± 0.26, and 0.31 ± 0.26 territories/ha in redtop, no redtop, and control blocks, respectively. In 2002, mean territory density across both sites was 0.46 ± 0.66, 0.56 ± 0.17, and 0.12 ± 0.17 territories/ha; there were no blackbird territories in redtop or control blocks at Plowboy Bend during this year. Territory density did not differ among blocks or years (likelihood ratio test: $\chi^2 = 5.8$, df = 3, $P = 0.12$).

We did not find differences among the three block types for mean perch density, mean total vertical cover, or mean vertical grass cover (Fig. 1A, C, E). The model for mean perch height differed significantly from the null model ($\chi^2 = 39.0$, df = 3, adj. $P < 0.001$), but the differences were among years (2001: 2.16 ± 0.03 m; 2002: 1.82 ± 0.04 m; $t = 6.73$, df = 74, $P < 0.001$); there were no differences in perch height among blocks (Fig. 1B). Similarly, models for mean threshold nest-cover height and grass height differed from null models, but again differences were among years rather than blocks (threshold nest-cover height model: overall $\chi^2 = 17.0$, df = 3, adj. $P < 0.01$; mean grass height model: overall $\chi^2 = 28.6$, df = 2, adj. $P < 0.008$; Fig. 1D, F). Mean grass height across all territory blocks was greater in 2001 (2001: 0.53 ± 0.02 m; 2002: 0.36 ± 0.02 m; $t = 5.53$, df = 74, $P < 0.001$), whereas mean threshold nest-cover height was shorter in 2001 (2001: 0.40 ± 0.06 m; 2002: 0.63 ± 0.06 m; $t = -4.30$, df = 74, $P < 0.001$).

We used samples from 35 Red-winged Blackbird breeding territories and 35 unused plots (2002 data only) to compare vegetation in breeding territories with that in unused plots ($n = 10$, 13, and 12 unused plots sampled from both sites combined in redtop, no redtop, and control blocks, respectively). Models testing for differences between territories and unused plots did not differ from

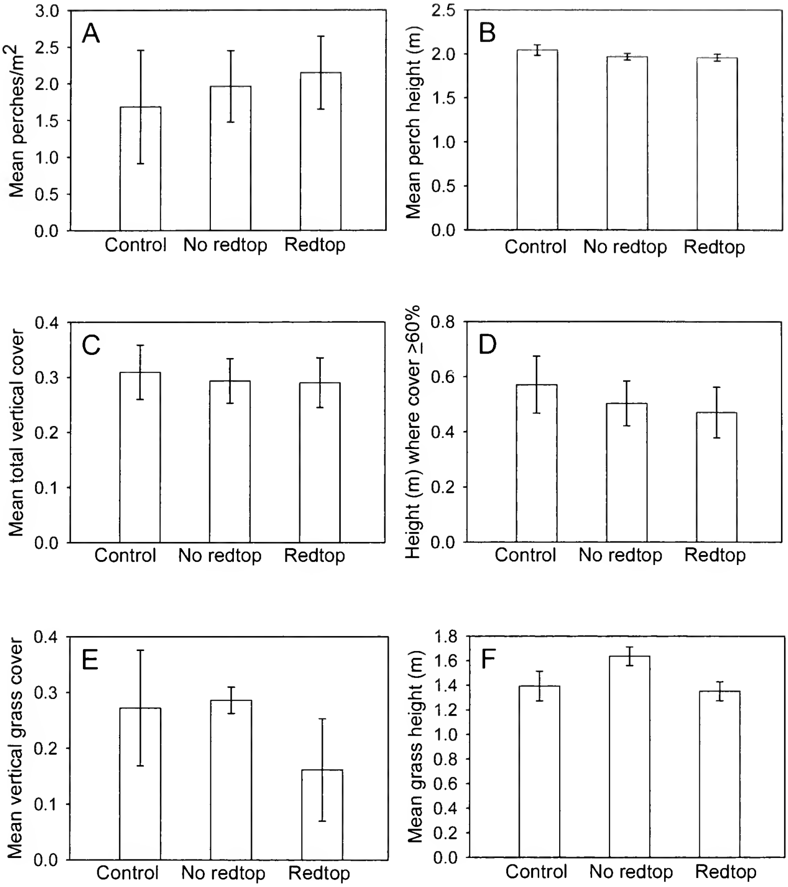

FIG. 1. Vegetation cover (expressed as a proportion), height, and perch density comparisons (±SE) among treatment blocks at Plowboy Bend and Smoky Waters Conservation Areas, Missouri, 2001–2002.

null models with respect to perch height (Fig. 2B), mean total vertical cover (Fig. 2C), or threshold nest-cover height (Fig. 2D). Overall, mean perch density varied among combinations of block and territory or unused plots ($\chi^2 = 28.5$, df = 4, adj. $P < 0.008$; Fig. 2A). Territories in control blocks had greater perch densities than in all other block types, although there were only four control territories in the analysis (all adj. $P \leq 0.005$; Fig. 2A). Perch densities did not differ between other combinations of block and territory or unused plots, except that perch densities were greater in no redtop territories than they were in redtop territories and redtop unused plots (no redtop territories versus redtop territories: $t = 3.42$, df = 61, adj. $P < 0.005$; no redtop territories versus redtop unused plots: $t = 3.01$, df = 61, adj. $P < 0.006$).

Overall, mean vertical grass cover varied among combinations of block and territory or unused plots ($\chi^2 = 21.5$, df = 5, adj. $P < 0.01$). Grass cover was greater in no redtop territories compared with no redtop unused plots, control unused plots, and redtop territories and unused plots (all adj. $P \leq 0.004$; Fig. 2E). Grass height varied overall among combinations of block and territory or unused plots ($\chi^2 = 15.4$, df = 5, adj. $P < 0.01$). Grass height was greater in no redtop territories than in redtop, no redtop, and control unused plots (all adj. $P \leq 0.004$; Fig. 2F).

DISCUSSION

We found no significant differences in territory density or area among treatment blocks, nor did we find differences among vegetation variables by territory treatment block when

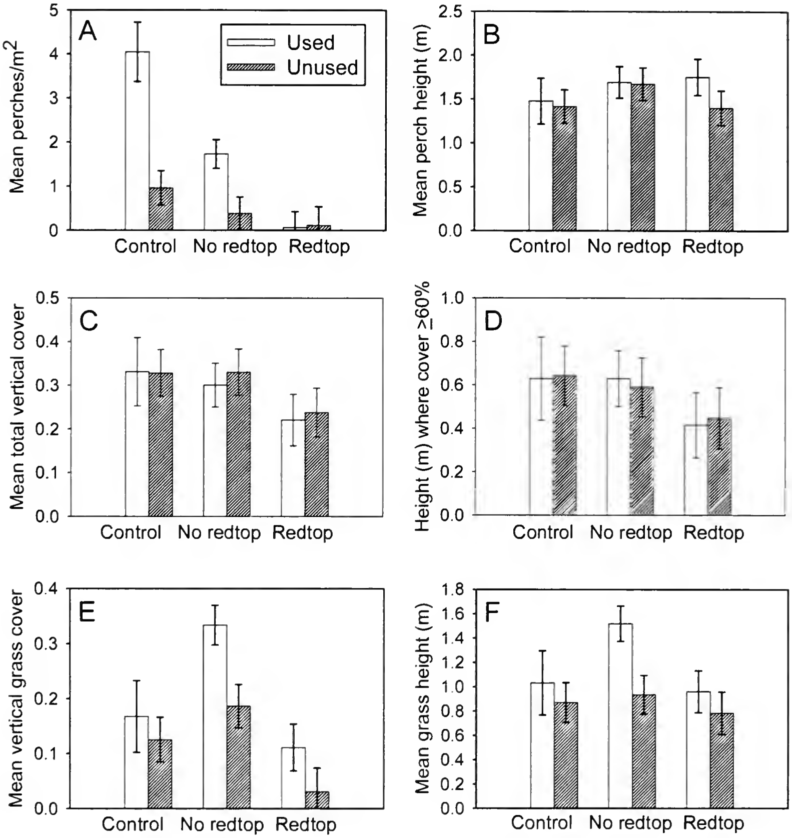

FIG. 2. Vegetation cover (expressed as a proportion), height, and perch density comparisons (±SE) of Red-winged Blackbird territories (used) and unused plots at Plowboy Bend and Smoky Waters Conservation Areas, Missouri, 2002.

2001 and 2002 data were combined. We did find differences, however, between territories and unused plots; generally, blackbird territories were characterized by denser or taller grass cover than unused plots, and territories in control and no redtop blocks tended to contain more perches than unused plots.

In the analysis of territories versus unused plots, the greater perch density in territory blocks with no cover crop (no redtop and control blocks) compared with those that had a cover crop (redtop) may be a reflection of redtop's ability to suppress invasion by trees and shrubs. However, perch density did not differ among territory blocks or years when data from both years were combined (Fig. 1A), whereas the territory/unused analysis, which included only 2002 data, revealed extreme differences in perch density among territory blocks (Fig. 2A). In the case of control territories, perch density could have been an artifact of small sample size, as there were only 4 territories in control blocks in 2002 compared to 10 in 2001. However, upon visual inspection, we detected similar between-year differences in mean perch density in redtop blocks (Fig. 1A versus 2A), and in this case sample sizes were 19 and 14 in redtop territories in 2001 and 2002, respectively. Such inter-annual inconsistencies in bird-vegetation relationships are common and often prevent researchers from reaching direct conclusions in studies of avian-habitat associations (Riffell et al. 2001), including studies of Red-winged Blackbirds (Erckmann et al. 1990) and other blackbirds (Orians and Wittenberger 1991). Red-winged Blackbirds may require only a few perches for territory defense. We noted that blackbirds typically reused the same perches, sometimes frequenting only four or five perches repeatedly (MAF pers. obs.). It may be that perch availability limits blackbird territory settlement only at some lower threshold, in which case even territories with very low perch densities at our sites (e.g., redtop; Fig. 2A) may have met this requirement. Perches have been shown not to limit habitat use by some songbirds (Vickery and Hunter 1995), but at least one study suggests that they are necessary for Red-winged Blackbirds; Joyner (1978) found that even in areas with a preferred grass cover type, blackbirds did not establish territories if fence posts—used as perches—were totally lacking.

In addition to variation in perch density, we also found differences in grass cover and height between territories and unused plots within and among treatment blocks. Variable grass cover, at least within no redtop blocks, suggests that blackbirds may have settled in a non-uniform fashion with regard to grass patches. Although our data did not permit us to relate territories to grass patchiness spatially, overall we did not notice obvious patterns in territory settlement; there were two possible exceptions: (1) the only two blackbird territories in the Plowboy Bend redtop block were very close to blackbird territories on the adjoining no redtop block, from which forbs, shrubs, and Johnsongrass had spread into the redtop block (MAF pers. obs.); and (2) blackbirds tended to avoid settlement along one edge of the Smoky Water control block (MAF pers. obs.). In the second case, we are not sure why blackbirds avoided the block edge, but we believe that settlement in redtop at Plowboy Bend may have been influenced both by the rampant growth of Johnsongrass and by redtop's ability to suppress Johnsongrass and other vegetation. Redtop cover was particularly uniform at Plowboy Bend, where blackbird use of the redtop block was minimal, whereas the redtop block at Smoky Waters underwent extensive invasion of shrubs and forbs (MAF and DEB pers. obs.). Johnsongrass, a dense, stout-stemmed grass that grows to 1.8 m high, was also used as a nesting substrate, whereas redtop was not. Of more than 250 Red-winged Blackbird nests found from 2001–2003, none were anchored in redtop grass, whereas Johnsongrass was among the five most commonly used nest substrates (DEB unpubl. data).

The pattern of denser and taller grass cover in territories, especially in no redtop blocks, generally agrees with other findings in studies of Red-winged Blackbirds. Bollinger (1995) believed that blackbirds occupied his upland sites due to the availability of suitable nest cover and vegetation with stems strong enough to support their nests; results of other studies also indicate that, where stout plants are available, blackbirds choose them as nest sites or for territorial activity (Albers 1978, Joyner 1978, Turner and McCarthy 1998, Kobal et al. 1999). Bollinger (1995) found a positive relationship between presence of grass and blackbirds, and Camp and Best (1994) found a positive relationship between grass cover and nest densities. Other studies have shown that Red-winged Blackbirds favor dense vegetation (LaPointe et al. 2003); Albers (1978) found that blackbird territories had significantly taller, denser vegetation than unused areas, and Bollinger (1995) found that Red-winged Blackbirds were most abundant in fields with dense cover. However, in a survey of Illinois grassland species, Herkert (1994) found no correlates of vegetation structure and occupancy by Red-winged Blackbirds, which were present on 93% of his transects, and Scott et al. (2002) found that blackbirds were negatively associated with grass cover on reclaimed surface mines in Indiana.

Although our 2002 data revealed differences in perch density when comparing territories with unused plots, our results suggest that perch density does not influence Red-winged Blackbird territory selection as long as perch density is above some lower limit. However, particularly in no redtop blocks, blackbirds tended to choose territories that had denser, taller grass cover than that observed in unused plots. This finding is in agreement with other studies, which have shown that Red-winged Blackbirds appear to favor dense vegetation (Albers 1978, Kobal et al. 1999), including tall or dense grass cover (Camp and Best 1994, Bollinger 1995).

ACKNOWLEDGMENTS

This work was funded through the University of Missouri's Center for Agroforestry under cooperative agreements 58-6227-1-004 with the Agricultural Research Service and C R 826704-01-2 with the U.S. Environmental Protection Agency (EPA). The results presented are the sole responsibility of the Principal Investigators and/or University of Missouri and may not represent the policies or positions of the EPA. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the view of the U.S. Department of Agriculture. Equipment and computer resources support were provided courtesy of University of Missouri-Columbia's Quantitative Silviculture Laboratory and the U.S. Department of Agriculture Forest Service North Central Research Station. We thank F. R. Thompson for statistical advice and M. A. Gold and D. C. Dey for support and professional considerations. Comments by G. H. Orians, K. Yasukawa, B. B. Steele, P. D. Vickery, and an anonymous reviewer greatly improved earlier versions of the manuscript. We gratefully thank field assistants H. Morris, H. Heitz, A. Schultz, and T. Altnether for data collection.

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THE USE OF SOUTHERN APPALACHIAN WETLANDS BY BREEDING BIRDS, WITH A FOCUS ON NEOTROPICAL MIGRATORY SPECIES

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ABSTRACT.—Although loss of wetlands in southern Appalachia has been especially severe, no avian studies have been conducted in the vestiges of these ecosystems. Our research assessed avian use of southern Appalachian wetlands in the breeding seasons of 1999 through 2001. Site analyses included 18 habitat variables, including total wetland area, area of open water, beaver or livestock evidence, edge type (abrupt or gradual), and percent cover of nine vegetation types. We analyzed avian species richness and abundance at the community level and in guilds based on migratory status and breeding habitat preference. Measures of vegetation and habitat—particularly those resulting from beaver activities—and gradual edges were significantly correlated with guild- and community-level variables. Evidence of beaver (i.e., forest gaps where trees had been felled, ponds where drainages had been dammed; hereafter referred to simply as "beaver evidence") was significantly correlated with greater community-level species richness and abundance. Both beaver evidence and gradual edge were positively associated with greater species richness and abundance of Neotropical migratory birds (NTMBs) overall, as well as with the late-successional NTMB guild. Presence of gradual edge alone also was significantly correlated with high abundance of birds in the early-successional NTMB guild. Beaver and gradual edge may have contributed to higher-quality breeding habitats with relatively greater overall productivity and structural complexity in some wetlands. *Received 24 November 2004, accepted 22 March 2006.*

Wetlands of the southern Appalachians are perhaps the rarest and most threatened in the southeastern U.S. Weakley and Shafale (1994) estimate that only one-sixth (about 2,000 ha) of the bogs in pre-European settlement southern Appalachia remain today. Historically, post-glacial southern Appalachian wetlands have been maintained by precipitation, groundwater recharge, and natural suppression of woody vegetation (Weakley and Shafale 1994, Lee and Norden 1996); humans, however, have since altered the woody vegetation. Pleistocene megafauna (Weigl and Knowles 1995, Lee and Norden 1996), including elk (*Cervus elaphus*) and American bison (*Bison bison*; Lee and Norden 1996, but see Ward 1990) are believed to have maintained these wetlands in early-successional states via browsing, but all have disappeared concomitant with human settlement. Native American use of fire also may have suppressed the encroachment of woody vegetation (Lee and Norden 1996) into southern Appalachian wetlands (Delcourt and Delcourt 1997). Today, fires are suppressed and quickly extinguished when they do occur (Weakley and Shafale 1994). Widespread loss of beaver (*Castor canadensis*) via the fur trade of the 18th and 19th centuries also reduced the development (Snodgrass 1997) and maintenance of wetlands throughout the landscape (Webster et al. 1975, Naiman et al. 1988, Weakley and Shafale 1994, Lawton and Jones 1995, Lee and Norden 1996). Most recently, the majority of remaining small wetlands in southern Appalachia have been converted to pasture, developed, or manipulated for other human uses (Weakley and Shafale 1994).

Today, the remaining wetlands of southern Appalachia are considered biological hotspots (Murdock 1994); until now, however, no study had focused on the breeding avifauna of these ecosystems. Southern Appalachia's wetlands are important to breeding Neotropical migratory birds (NTMBs). In fact, parts of the region harbor the greatest species richness and abundance of NTMBs in North America (Simons et al. 2000); however, the region's populations of NTMBs are declining more rapidly than anywhere else in North America (Rodriguez 2002). Species preferring open, early-successional habitats or late-successional for-

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ests are undergoing the most rapid declines (Robbins et al. 1989; reviewed in Askins et al. 1990). Of NTMBs that breed in southern Appalachia's early-successional habitats, 76% are declining (Hunter et al. 2001, Thompson and DeGraaf 2001) due to losses of early successional grasslands, scrub-shrub, open-canopy woodlands, and small canopy gaps (Hunter et al. 2001); some of North America's greatest declines in early-successional species have been reported from southern Appalachia (Franzreb and Rosenberg 1997).

Declines among NTMBs that breed in late-successional habitats are due, in part, to forest fragmentation resulting from agricultural, residential, and commercial development (Robbins et al. 1989, Askins et al. 1990, Faaborg et al. 1995). Forest-interior species suffer from increased rates of brood parasitism (Brittingham and Temple 1983, Robbins et al. 1989) and nest predation (Askins et al. 1990), and from increased competition with other bird species (Askins et al. 1990, Zannette et al. 2000) in the smaller habitat patches that result from fragmentation. Although the southern Appalachians contain approximately 80% of the primary forests in the eastern U.S. (Davis 1993), more species are declining in the region (42% of forest-breeding species) than in North America as a whole (27%; Franzreb and Rosenberg 1997).

In southern Appalachia, wetland loss has been concurrent with declines in NTMB populations, although it has not been evaluated as a contributing factor (Hunter et al. 1999). In southern Appalachian wetlands, habitat succession ranges from open, early-successional grasslands to late-successional, forested bogs; thus, these wetlands may provide important breeding habitats for both early- and late-successional breeding species, some of which are undergoing the greatest rates of population decline.

Considering the general scarcity of southern Appalachian wetlands and the disproportionately high rates of decline among NTMB species in that region, research on the use of southern Appalachian wetlands by breeding birds is overdue. Herein, we report the results of such research, focusing specifically on the habitat characteristics that make certain kinds of wetlands attractive to NTMBs in early- and late-successional habitat guilds of breeding birds.

METHODS

Study sites.—We collected data at 57 southern Appalachian wetlands in western North Carolina (n = 44), northeastern Tennessee (n = 3), and southwestern Virginia (n = 10). Wetland elevations ranged from 442 to 1,254 m. The total wetland area in our study was 795 ha. Individual wetland area ranged from 0.40–95 ha (mean = 14 ha); excluding the four largest wetlands, however, mean wetland size was only 0.64 ha. Such small wetland areas are typical in regions of high topographic relief.

All wetland sites were dominated by hydrophytic vegetation and other hydrologic features (i.e., hydric soils, periodic to permanent inundation and/or soil saturation). Forty-four of our sites were used in previous botanical and herpetofaunal studies; we located the others by using natural history records from the North Carolina Natural Heritage Program and the North Carolina Museum of Natural Sciences. All wetlands were classified as one of three palustrine system types (Cowardin et al. 1979): emergent (n = 23), scrub-shrub (n = 21), or forested (n = 13).

Some of our study wetlands were low-pH, precipitation-fed bogs, wherein peat-filled depressions were dominated by a lattice of sphagnum mats and standing water. In these open wetlands, woody vegetation was scarce, although some had a sparse shrub layer (e.g., *Salix* spp., *Alnus* spp., and *Acer rubrum* saplings). Other study wetlands were groundwater-sourced fens characterized by thick covers of mosses, lichens, grasses, and forbs. Most study wetlands were located in floodplains and characterized by a diverse, structurally complex vegetative community. These floodplain wetlands were often the result of historic or current beaver activity and may have been groundwater and/or surface-water fed, though detailed hydrologic characteristics of study sites were not addressed.

All wetlands were owned by Appalachian State University (ASU; n = 2), the Blue Ridge Parkway National Park (BRP; n = 22), The Nature Conservancy (TNC; n = 6), the North Carolina Department of Transportation (NCDOT; n = 2), the U.S. Department of Agriculture Forest Service (USFS; $n = 3$), or private landowners ($n = 22$). (Hereafter, all sites other than those owned by private landowners will be referred to as "publicly owned sites," including TNC sites, although we recognize that technically, TNC sites are "private.")

In general, publicly owned wetlands are actively managed, whereas privately owned sites are not. Publicly owned wetlands were characterized by fewer land-use disturbances than those that were privately owned, and they were managed for their persistence in the landscape. Privately owned sites generally displayed one or more effects of land use, such as logging, grazing, and mowing, or draining for agriculture, residential development, and/or commercial development.

Small southern Appalachian wetlands are inherently associated with edges, and we classified site edges as either abrupt or gradual. Our qualitative classification of edge type followed that used in other studies of edge-type effects on breeding birds (Suarez et al. 1997, Luck et al. 1999). An abrupt edge displayed a distinct, drastic change in vegetation structure between two vegetation types. Abrupt edges ($n = 29$ sites) usually resulted from persistent land uses, such as mowing or cattle grazing, thus creating a sharp edge between grasses/forbs and forest. In some sites, beaver also had created abrupt edges. For example, sites recently flooded by beaver dams often had no transitional vegetation structure between the new pond and the canopy-level vegetation (Snodgrass 1997).

Twenty-eight sites had a gradual edge, qualitatively defined as a smooth gradient between vegetation types or successional stages (Suarez et al. 1997, Luck et al. 1999). Gradual edges comprised a complex transition between vegetation types, where grasses, forbs, saplings, and shrubs were intermixed. Most of the beaver-impacted wetlands in our study had gradual edges, primarily because there had been sufficient time since beaver invasion for succession to occur; gradual edges did occur in the absence of beaver evidence wherever edges were not maintained by anthropogenic disturbances.

Presence/absence of beaver evidence was assessed via visual observation. Some beaver-impacted wetlands were inundated hardwood forests. Others were inundated gaps in the canopy that had resulted from tree-felling and damming activities; these wetlands often contained much downed, coarse woody debris and many exposed stumps. Some beaver-impacted wetlands had been abandoned, as evidenced by breached dams and exposed sediments, which supported a variety of grasses, forbs, and shrub species (i.e., "beaver meadows"). Overall, beaver-impacted wetlands were characterized by a diversity of successional seres associated with beaver colonization and abandonment.

Avian censusing.—During the 1999 field season, we conducted a pilot study to compare spot mapping and 50-m fixed-radius point counts. Fixed-radius point counts were superior for this study, as they generated more bird detections in less time than spot-mapping (Ralph et al. 1993), allowing us to increase sample size by visiting more wetlands in 2000 and 2001. Thus, during the breeding seasons of 2000 and 2001, we conducted three 10-min, 50-m fixed-radius point counts in each of the 57 wetlands ($n = 33$ sites in 2000 and $n = 24$ sites in 2001). All point counts were conducted between 15 May and 30 June, from sunrise to 10:00 EST, on days when neither precipitation nor wind conditions interfered with bird detections (Ralph et al. 1995). During each visit, the point count was conducted from the center of the core wetland area (Ralph et al. 1995) and always at the same point location (Johnson 2001). We recorded all birds seen or heard during each count (Ralph et al. 1995), and bird detections were categorized as <25.0, 25.1–50.0, and >50.0 m from the point-count center. The same observer conducted all point counts in all 3 years.

Although point counts—by virtue of standardized and routinely adopted protocols (Ralph et al. 1995)—have become the conventional technique for conducting avian censuses, differences in the detectability of different species may generate inaccurate counts (Thompson 2002). Statistically based detectability adjustments are sometimes used to attempt to compensate for these errors (e.g., double-observer approach, Nichols et al. 2000; distance sampling, Rosenstock et al. 2002; double sampling, Bart and Earnst 2002). We used raw data for our analyses because our sample size ($n = 57$ wetlands over

3 years) and data did not meet all the assumptions necessary for use of distance-sampling methods (Hutto and Young 2003). In addition to our small sample size, we could not be certain that every individual present was counted only once or that precise distances for all detections were estimated accurately. Thus, our raw data were used to assess possible relationships between habitat and bird communities in this short-term study.

We used the number of species and individuals recorded at point counts to calculate community- and guild-level dependent variables for statistical analyses. For each wetland, we calculated community-level species richness as the total number of species observed across all three visits. Therefore, species richness assesses all species observed using a wetland, whether or not they were breeding there; some birds using wetlands for foraging (Pagen et al. 2000) or for extraterritorial copulation forays (Norris and Stutchbury 2001) may not have been present during all census visits. For each wetland, we also calculated community-level avian abundance as the mean number of birds observed during all three visits.

To develop guild-level variables, we assigned all bird species to guilds based upon classifications used by the Breeding Bird Survey (Sauer et al. 2001). We focused on the NTMB guild (as opposed to residents and short-distance migrants). We further classified the NTMBs into two breeding-habitat guilds: "late-successional" (i.e., woodland) and "early-successional" habitats. All early-successional NTMBs nest in scrub, except the Eastern Meadowlark (*Sturnella magna*)—the only "grassland" nester that we observed. Because Eastern Meadowlarks represent a unique subguild of early-successional breeders, and because we observed them in only six sites, we excluded this species from our analyses. Thus, within each of the three guilds (i.e., NTMB and two habitat guilds), we calculated species richness and abundance, which we used as dependent variables in statistical analyses. For each wetland, we calculated within-guild species richness as the total number of species in each guild observed across the three point counts. We calculated within-guild abundance as the mean number of individuals in each guild detected across all three visits.

Vegetation analyses.—At each site, we recorded wetland class (Cowardin et al. 1979), presence or absence of livestock evidence, presence or absence of beaver evidence, edge type, and ownership status; these categorical variables were employed as independent variables in statistical analyses (Table 1). For a given wetland, vegetation sampling and avian censuses were conducted in the same breeding season (following the protocol described in Hamel et al. 1996). At each wetland, all data were collected from an 11.28-m-radius circle surrounding the point-count center (see table 1 in James and Shugart 1970).

Percent cover of several classes of vegetation structure and open water (Table 1) were estimated by using an ocular tube (Hamel et al. 1996). In each of the four cardinal directions, we measured 2, 4, 6, 8, and 10 m from the point-count center. At each of these points we looked downward and upward through a 5.08-cm ocular tube. Presence of vegetation structural layer(s) observed within the field of view of the ocular tube were recorded and used to calculate the percent cover of vertical structural layers in the vegetation plot.

We used a vegetation profile board to assess horizontal vegetation structure in each wetland (Hamel et al. 1996). This method entails using a profile board (50.8 × 50.8 cm) that is divided into a grid of 25 equally sized squares. The board was placed vertically on the ground, 10 m from, and facing, the point center. We recorded number of squares fully visible at 0, 2.5, 5, and 7 m from point center, in each of the cardinal directions. A simple calculation using the number of obstructed squares (across all distances and directions) was used to estimate percent horizontal vegetation density in each wetland (Hamel et al. 1996).

Data analysis.—We used SAS (SAS Institute, Inc. 2000) to conduct stepwise multiple linear regressions (SMLR) with the PROC GLM program for among-site analyses of wetland use by breeding birds at the community and guild levels. Species richness and total abundance values calculated from point-count data were our dependent variables, and vegetation and habitat data collected from each wetland were independent variables. Because data from 2000 and 2001 did not differ (*t*-tests), we pooled data from both years.

TABLE 1. Description of 18 independent variables measured in 57 southern Appalachian wetlands during 2000 and 2001.

Independent variables	Method of measurement
Wetland class	Persistent-emergent, scrub-shrub, or forested (Cowardin et al. 1979)
Livestock evidence	Presence or absence of recent livestock activity (i.e., livestock, trampling, and/or manure)
Edge type	Edge nearest the point-count center was gradual or abrupt
Beaver evidence	Presence or absence of recent beaver activity (i.e., actively maintained dams, freshly felled trees, and/or recently gnawed stumps)
Ownership status	Publicly or privately owned
Blue Ridge Parkway ownership status	Under the jurisdiction (or not) of Blue Ridge Parkway National Park
Size of wetland	Publicly owned sites: information obtained from managers; privately owned sites: estimated (to the nearest 0.1 ha) from 1:24,000 USGS topographic maps
Open water	Percent cover of open water[a]
Stem density of snags	No. snags >10 cm dbh[b]
Stem density of live trees	No. trees >10 cm dbh[b]
Basal area of live and dead trees (cm^2)	Total basal area of trees >10 cm dbh[b] (measured with a Biltmore stick; Hamel et al. 1996)
Canopy cover	Percent canopy cover[a,b]
Midstory cover	Percent cover of total midstory vegetation[a,b]
Shrub cover	Percent cover of shrub vegetation[a,b]
Ground cover	Percent ground cover[a,b]
Forb cover	Percent cover of forb vegetation[a,b]
Grass cover	Percent cover of grass vegetation[a,b]
Vegetation profile	Estimated horizontal density of vegetation[a,b]

[a] Vegetation measures made using the ocular tube method (Hamel et al. 1996).
[b] Measurements taken within 11.28-m circular sample plots.

We checked all dependent and independent variable distributions for outliers using box plots and normal probability plots (Tabachnick and Fidell 1983, Zar 1999). Outlying values for independent variables were confirmed not to have resulted from data entry errors, and were retained for final regression analyses. We also checked all variables for normality using residual scatterplots (Tabachnick and Fidell 1983, Zar 1999) obtained by running preliminary multiple regression models for every dependent variable against all raw data for the independent variables (SAS Institute, Inc. 2000). Residual scatterplots for all dependent variables were normal, and regression models for all dependent variables were considered valid.

Prior to running final regression analyses, we conducted a correlation analysis on all independent variables to eliminate redundancy in habitat measurements. In cases where correlations were ≥ 0.50, we removed one of the variables before running final regression analyses. For regression models, categorical variables, such as evidence of beaver activity, edge type, and wetland type, were assigned absence/presence values of 0 or 1, respectively. Only parameters significant at $P < 0.05$ were included in final regression models.

RESULTS

During the 2000 and 2001 breeding seasons, we conducted 171 point counts in the 57 study wetlands and detected 2,266 birds representing 90 species (see Appendix for species observed).

Community-level analyses.—Presence of gradual edges, beaver evidence, and private ownership collectively explained 50% of the variation in community species richness of NTMBs (Table 2). Beaver evidence also explained 16% of community abundance, and abundance associated with wetlands on the BRP was lower than it was at wetland sites elsewhere (Table 2).

Guild-level analyses.—Species richness of NTMBs was explained by the presence of gradual edge (42.5% of variation) and evidence of beaver activity (7%; Table 3). Percent ground cover was also positively corre-

TABLE 2. Significant ($P < 0.05$) predictors of community-level avian use at 57 southern Appalachian wetlands during the breeding seasons of 2000 and 2001.

Community-level parameter	Predictor	F	SE	Parameter r^2	Model R^2
Species richness[a]	Gradual edge	23.51	0.96	0.300***[b]	
	Beaver evidence	10.15	1.13	0.111**	0.41**
	Ownership status	9.66	0.96	0.091**	0.50**
Mean avian abundance[c]	Beaver evidence	10.11	4.64	0.155**	
	BRP status	7.05	3.97	0.098*	0.25*

[a] Total number of species detected in all three point counts in each wetland.

[b] $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

[c] Mean number of individuals observed during three point-count visits to each study wetland.

lated with species richness, although percent grass cover was negatively associated with species richness (Table 3). As with NTMB richness, NTMB abundance was most strongly associated with gradual edge and evidence of beaver activity; collectively, these variables explained 37% of the model variation. Also, though to a lesser degree, NTMB abundance was positively associated with percent cover of canopy vegetation (Table 3).

Basal area of trees at our sites had the strongest negative effect on species richness and abundance of early-successional NTMBs: it explained 16% of the variation in both richness and abundance models (Table 4). Early-successional NTMB species richness and abundance were positively correlated with grazing and gradual edge, respectively (Table 4). Late successional NTMB species richness and abundance both were positively associated with gradual edge, basal area, and evidence of beaver activity (Table 4). In addition, species richness of late-successional NTMBs was positively associated with canopy cover (accounting for 19% of the variation) and abundance was positively associated with midstory cover (accounting for ~5% of the variation) (Table 4).

DISCUSSION

Although our vegetation sampling areas (11.28-m-radius circular plots) did not correspond exactly with our avian census areas (50-m-radius circular plots), the wetland sizes were small, in which case our quantitative vegetation measurements should have adequately represented the vegetation of most wetlands overall; only the largest wetlands may have been represented inadequately in our 11.28-m vegetation plots. We recognize that this spatial inconsistency may have driven the effects of our qualitative habitat variables (i.e., evidence of beaver activity, edge type) more than the continuous variables (e.g., percent cover of vegetation types) in our regression models. However, relationships between avian community structure and vegetation structure should not be disregarded.

In general, many of our results support existing hypotheses about the effects of land use and environmental variables on NTMB species richness and abundance. At the community and guild levels, species richness and abundance were associated with various habitat characters that can be explained by the habitat preferences of late- and early-succes-

TABLE 3. Significant ($P < 0.05$) predictors of southern Appalachian wetland use by the Neotropical migratory bird (NTMB) guild during the breeding seasons of 2000 and 2001.

Guild-level parameter	Predictor	F	SE	Parameter r^2	Model R^2
NTMB species richness	Gradual edge	40.59	0.62	0.425***[a]	
	Grass cover (%)	4.37	0.01	0.078**	0.50**
	Beaver evidence	7.93	0.83	0.074**	0.576**
	Ground cover (%)	9.68	1.03	0.033*	0.609*
NTMB abundance	Gradual edge	21.53	2.37	0.284***	
	Beaver evidence	7.83	2.80	0.090**	0.374**
	Canopy cover (%)	4.53	0.06	0.063*	0.436*

[a] $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

TABLE 4. Significant ($P < 0.05$) predictors of southern Appalachian wetland use by early-successional (ES-NTMB) and late-successional (LS-NTMB) Neotropical migratory bird guilds during the breeding seasons of 2000 and 2001.

Guild-level parameter	Predictor	F	SE	Parameter r^2	Model R^2
ES-NTMB species richness	Basal area	10.14	0.00	0.156**[a]	
	Livestock evidence	11.47	0.38	0.148**	0.304**
ES-NTMB abundance	Basal area	10.45	0.01	0.160**	
	Gradual edge	10.84	1.33	0.141**	0.300**
LS-NTMB species richness	Gradual edge	32.60	0.66	0.372***	
	Canopy cover (%)	22.58	0.02	0.185***	0.557***
	Beaver evidence	8.94	0.73	0.064**	0.621**
	Basal area	4.68	0.00	0.031*	0.652*
LS-NTMB abundance	Basal area	40.45	0.01	0.424***	
	Beaver evidence	18.19	1.80	0.145***	0.569***
	Midstory cover (%)	6.40	0.06	0.046*	0.615*
	Gradual edge	4.22	1.62	0.029*	0.644*

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

sional NTMBs. The positive association between private ownership and species richness, however, was unexpected. Although many of the publicly owned wetlands we studied are managed, in part, to promote biodiversity, our results show that private wetlands had greater community-level species richness than sites held in public trust. This may reflect landscape-level influences. We suspect that publicly owned sites often were surrounded by less fragmented landscapes than privately owned sites, which often were embedded in landscapes fragmented by various land uses. The relatively greater number of small habitat patches surrounding privately owned wetlands might have generated a greater diversity of habitats that supported a greater variety of birds (Whitcomb et al. 1981).

The positive effects of gradual edges on the avian community overall, and on NTMBs, were also unexpected. Numerous studies have shown that, in fragmented forest landscapes with high edge-to-interior ratios, area-sensitive NTMBs experience increased predation due to greater predator abundance (Temple and Cary 1988, Wilcove and Robinson 1990, Faaborg et al. 1995) and species richness (Forsyth and Smith 1973, Heske 1995, Chalfoun et al. 2002), as well as greater rates of brood parasitism (Brittingham and Temple 1983, Johnson and Temple 1990). However, the differential effects of gradual versus abrupt edges on NTMBs have received far less attention.

Authors of previous studies have reported greater rates of nest predation along abrupt edges than in gradual edges; they further propose that the more developed vegetation structure in gradual edges provides superior nest concealment (Ratti and Reese 1988) and minimizes the activity and efficiency of predators (Luck et al. 1999). Gradual edges may also provide foraging benefits. Lopez de Casenave et al. (1998) found greater avian species richness and abundance in "mature," or gradual, edges than in surrounding habitats. They concluded that complex, mature edges provided greater fruit production and more foraging niches for birds. Along with these findings, our results suggest that further assessments of parasitism, predation, and foraging efficiency in abrupt versus gradual edges may help determine why edge structure can affect avian community structure.

Overall structure of wetland vegetation affected by beaver activity also may have influenced southern Appalachian bird communities. Grover and Baldassarre (1995) found that wetlands actively maintained by beaver harbored greater species richness of breeding NTMBs and woodland species than other wetlands, primarily due to their structurally diverse edges. In our study, beaver-impacted wetlands were characterized by gradual edges more often than by abrupt edges ($P < 0.05$, $R^2 = 0.302$).

Beaver activity is also thought to enhance avian foraging efficiency by creating structurally diverse habitats with a diversity of foraging niches (Medin and Clary 1990) and by increasing the productivity of insects—the dominant component of NTMB diets (Reese and Hair 1976). Further investigations focusing on differences in wetland vegetation structure and productivity in beaver-impacted versus other wetlands could provide more conclusive results regarding how beaver may enhance habitat quality for nesting NTMBs.

From a management perspective, results from our study and those of previous studies suggest new approaches to managing southern Appalachian wetlands to promote persistence of native birds. "Gradualizing" wetland edges and encouraging beaver could be especially beneficial for NTMBs. Edges are inherent results of current land-use practices, and although the effects of edge quantity on area-sensitive songbirds are well-documented, a better understanding of how edge quality affects these species may help to refine management activities.

Future investigations of how beaver benefit songbirds at local and landscape levels also might be prudent. Paradoxically, populations of avian species with very different habitat requirements are in decline, including those that prefer both early-successional grasslands and late-successional forests. Some researchers have argued that landscapes in the southeastern United States have lost their heterogeneity and are now dominated by homogeneous stands of mid-successional forest (Hunter et al. 2001). Prior to their near extirpation over a century ago, the estimated 60 million beaver in North Carolina alone (McGrath and Summer 1992) would have generated a remarkable mosaic of early- to late-successional ponds, meadows, and forested bogs. The physiographic diversity of these sites, coupled with their productivity, may have benefited bird species with a wide range of resource requirements. Rather than treating beaver as pests, public land managers in the southern Appalachians should encourage beaver in their efforts to restore a heterogeneous landscape capable of supporting a diverse avifauna.

ACKNOWLEDGMENTS

The U.S. Fish and Wildlife Service, Explorer's Club, Wilderness Society, and Appalachian State University Graduate School funded this research. We thank N. Murdock, D. Lee, C. Haney, and D. Herman for sharing their expertise and knowledge of the natural history, flora, and fauna of southern Appalachian wetlands. This study could not have been conducted without the cooperation of The Nature Conservancy, the National Park Service, the U.S. Department of Agriculture Forest Service, and various private landowners who allowed us access into highly sensitive areas to collect data. We would also like to thank the three anonymous reviewers of this manuscript for their helpful comments and suggestions.

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APPENDIX. Occurrence rates of bird species observed in 57 southern Appalachian study wetlands during 2000 and 2001.

Common name	Scientific name	No. sites where observed (%)
Wood Duck	*Aix sponsa*	2 (3.51)
Mallard	*Anas platyrhynchos*	1 (1.75)
Ruffed Grouse	*Bonasa umbellus*	1 (1.75)
Northern Bobwhite[a,b]	*Colinus virginianus*	1 (1.75)
American Bittern[a]	*Botaurus lentiginosus*	1 (1.75)
Green Heron[a]	*Butorides virescens*	1 (1.75)
Turkey Vulture	*Cathartes aura*	4 (7.02)
Red-tailed Hawk	*Buteo jamaicensis*	1 (1.75)
Killdeer[a]	*Charadrius vociferus*	1 (1.75)
Mourning Dove[a]	*Zenaida macroura*	6 (10.53)
Chimney Swift[a,b]	*Chaetura pelagica*	1 (1.75)
Ruby-throated Hummingbird	*Archilochus colubris*	11 (19.30)
Belted Kingfisher[a]	*Ceryle alcyon*	10 (17.54)
Red-bellied Woodpecker	*Melanerpes carolinus*	6 (10.53)
Yellow-bellied Sapsucker[c]	*Sphyrapicus varius*	3 (5.26)
Downy Woodpecker[b]	*Picoides pubescens*	12 (21.05)
Hairy Woodpecker	*Picoides villosus*	11 (19.29)
Northern Flicker[a,b]	*Colaptes auratus*	2 (3.51)
Pileated Woodpecker	*Dryocopus pileatus*	3 (5.26)
Eastern Wood-Pewee[a,b,c]	*Contopus virens*	12 (21.05)
Acadian Flycatcher[b,c]	*Empidonax virescens*	8 (14.04)
Alder Flycatcher[c]	*Empidonax alnorum*	14 (24.56)
Willow Flycatcher[a]	*Empidonax traillii*	9 (15.79)
Least Flycatcher[a]	*Empidonax minimus*	9 (15.79)
Eastern Phoebe[b]	*Sayornis phoebe*	21 (36.84)
Great Crested Flycatcher	*Myiarchus crinitus*	2 (3.51)
White-eyed Vireo	*Vireo griseus*	4 (7.02)
Blue-headed Vireo[c]	*Vireo solitarius*	16 (28.07)
Red-eyed Vireo	*Vireo olivaceus*	35 (61.40)
Blue Jay[a,b]	*Cyanocitta cristata*	11 (19.30)
American Crow	*Corvus brachyrhynchos*	21 (36.84)
Tree Swallow	*Tachycineta bicolor*	1 (1.75)
Bank Swallow	*Riparia riparia*	1 (1.75)
Barn Swallow	*Hirundo rustica*	1 (1.75)
Carolina Chickadee[a]	*Poecile carolinensis*	32 (56.14)
Tufted Timouse	*Baeolophus bicolor*	28 (49.12)
Red-breasted Nuthatch[c]	*Sitta canadensis*	2 (3.51)
White-breasted Nuthatch	*Sitta carolinensis*	10 (17.54)
Brown Creeper[c]	*Certhia americana*	1 (1.75)
Carolina Wren[b]	*Thryothorus ludovicianus*	17 (29.82)
House Wren	*Troglodytes aedon*	9 (15.79)
Winter Wren[c]	*Troglodytes troglodytes*	1 (1.75)
Golden-crowned Kinglet[c]	*Regulus satrapa*	7 (12.28)
Blue-gray Gnatcatcher[b]	*Polioptila caerulea*	6 (10.53)
Easten Bluebird	*Sialia sialis*	22 (38.60)
Veery[a]	*Catharus fuscescens*	4 (7.02)
Wood Thrush[a,b,c]	*Hylocichla mustelina*	12 (21.05)
American Robin[b]	*Turdus migratorius*	25 (43.86)
Gray Catbird[b,c]	*Dumetella carolinensis*	40 (70.18)
Northern Mockingbird[a]	*Mimus polyglottos*	2 (3.51)
Brown Thrasher[a]	*Toxostoma rufum*	8 (14.04)
European Starling[a]	*Sturnus vulgaris*	9 (15.79)
Cedar Waxwing	*Bombycilla cedrorum*	31 (54.39)
Golden-winged Warbler[a,c]	*Vermivora chrysoptera*	3 (5.26)
Northern Parula[c]	*Parula americana*	21 (36.84)
Yellow Warbler	*Dendroica petechia*	8 (14.04)

APPENDIX. Continued.

Common name	Scientific name	No. sites where observed (%)
Chestnut-sided Warbler[a,c]	*Dendroica pensylvanica*	17 (29.82)
Black-throated Blue Warbler[c]	*Dendroica caerulescens*	14 (24.56)
Yellow-rumped Warbler	*Dendrocia coronata*	1 (1.75)
Black-throated Green Warbler	*Dendroica virens*	2 (3.51)
Blackburnian Warbler[c]	*Dendroica fusca*	2 (3.51)
Pine Warbler	*Dendroica pinus*	3 (5.26)
Prairie Warbler[a,b]	*Dendroica discolor*	3 (5.26)
Black-and-white Warbler[b]	*Mniotilta varia*	10 (17.54)
American Redstart	*Setophaga ruticilla*	5 (8.77)
Worm-eating Warbler[c]	*Helmitheros vermivorum*	2 (3.50)
Swainson's Warbler[b,c]	*Limnothlypis swainsonii*	1 (1.75)
Ovenbird[b]	*Seiurus aurocapilla*	17 (29.82)
Louisiana Waterthrush[c]	*Seiurus motacilla*	7 (12.28)
Common Yellowthroat[a,b]	*Geothlypis trichas*	36 (63.16)
Hooded Warbler[c]	*Wilsonia citrina*	22 (38.60)
Canada Warbler[a,c]	*Wilsonia canadensis*	3 (5.26)
Yellow-breasted Chat[b]	*Icteria virens*	7 (12.28)
Scarlet Tanager[a,b,c]	*Piranga olivacea*	15 (26.32)
Eastern Towhee[a,b]	*Pipilo erythrophthalmus*	38 (66.67)
Chipping Sparrow[b]	*Spizella passerina*	10 (17.54)
Field Sparrow[a,b]	*Spizella pusilla*	13 (22.81)
Song Sparrow[a,b]	*Melospiza melodia*	41 (71.93)
White-throated Sparrow[a]	*Zonotrichia albicollis*	2 (3.51)
Dark-eyed Junco[a,c]	*Junco hyemalis*	16 (28.07)
Northern Cardinal	*Cardinalis cardinalis*	37 (64.91)
Rose-breasted Grosbeak[a]	*Pheucticus ludovicianus*	1 (1.75)
Indigo Bunting[a,b]	*Passerina cyanea*	42 (73.68)
Red-winged Blackbird[a]	*Agelaius phoeniceus*	21 (36.84)
Eastern Meadowlark[a,b]	*Sturnella magna*	5 (8.77)
Common Grackle	*Quiscalus quiscula*	4 (7.02)
Brown-headed Cowbird[a]	*Molothrus ater*	3 (5.26)
House Finch	*Carpodacus mexicanus*	6 (10.53)
American Goldfinch	*Carduelis tristis*	36 (63.16)
House Sparrow[a,b]	*Passer domesticus*	1 (1.75)

[a] Undergoing significant population decline throughout the species' breeding range (Sauer et al. 2001).

[b] Undergoing a moderate or significant population decline in southern Blue Ridge region (Partners in Flight physiographic region 23; Carter et al. 2000, Hunter et al. 1999) or in the Blue Ridge region of the North American Breeding Bird Survey (Sauer et al. 2001).

[c] Considered a priority species in the southern Blue Ridge region (Partners in Flight physiographic region 23; Carter et al. 2000, Hunter et al. 1999) or a species of local concern in the southern Appalachians (North Carolina Natural Heritage Program; LeGrand et al. 2001, Hunter et al. 1993, D. S. Lee and B. Browning unpubl. data).

Short Communications

The Wilson Journal of Ornithology 118(3):411–413, 2006

Breeding Range Extension of the Northern Saw-whet Owl in Quebec

Christophe Buidin,[1] Yann Rochepault,[1] Michel Savard,[2] and Jean-Pierre L. Savard[3,4]

ABSTRACT.—Although the breeding range of the Northern Saw-whet Owl (*Aegolius acadicus*) is restricted to North America, the northern limits of its range are still unclear. In Quebec, the most northerly confirmed breeding records had come from the Saguenay area (Chicoutimi; 48° 25′ N, 71° 03′ W) in balsam fir- (*Abies balsamea*) white birch (*Betula papyrifera*) forest and on the Gaspé Peninsula (Amqui; 48° 28′ N, 67° 25′ W) in balsam fir-yellow birch (*B. alleghaniensis*) forest. Between 1998 and 2003, however, we documented nine Northern Saw-whet Owl nests in balsam fir-black spruce (*Picea marina*) forest in boreal Quebec on the Mingan Terraces. These records extend the species' known breeding range northward to >50° N. *Received 8 August 2005, accepted 24 March 2006.*

The breeding range of the Northern Saw-whet Owl (*Aegolius acadicus*) is restricted to North America (Cannings 1993), and includes most of the southern Canadian forested areas, the mountainous regions of the United States, and the mountains of Mexico south to Oaxaca. The northernmost distribution of this species occurs along the Pacific coast, extending northward from British Columbia to south-central Alaska (American Ornithologists' Union 1998). However, the northern limit of its range remains unclear (Godfrey 1986, Cannings 1993). In Quebec, Northern Saw-whet Owls breed in all forested areas south of 49° N, with the exception of the Abitibi region (Côté and Bombardier 1996). Previously, the most northerly breeding records confirmed in Quebec came from the Saguenay area (Chicoutimi; 48° 25′ N, 71° 03′ W) in balsam fir- (*Abies balsamea*) white birch (*Betula papyrifera*) forest and on the Gaspé Peninsula (Amqui; 48° 28′ N, 67° 25′ W) in balsam fir-yellow birch (*B. alleghaniensis*) forest (Côté and Bombardier 1996). Seventeen records, however, in the 1979–1998 regional database housed at the Étude des populations d'oiseaux du Québec indicated that Northern Saw-whet Owls breed farther north in the Baie-Comeau area (49° 13′ N, 68° 09′ W) than what was published in the literature as their confirmed breeding range in Quebec (Côté and Bombardier 1996).

Between 1998 and 2003, we documented a northerly extension of the known breeding range of the Northern Saw-whet Owl in balsam fir-black spruce (*Picea marina*) forest in boreal Quebec, north of 50° N. During the 1997–1998 winter, we had erected 22 nest boxes for Boreal Owls (*Aegolius funereus*) in the Magpie River area (50° 19′ N, 64° 27′ W) and, during the 1998–1999 winter, we erected 51 nest boxes between the Manitou River (50° 19′ N, 65° 14′ W) and Longue-Pointe-de-Mingan (50° 17′ N, 64° 03′ W). From 1998 to 2003, we documented 9 Northern Saw-whet Owl nests (Table 1), as well as 15 Boreal Owl and 11 American Kestrel (*Falco sparverius*) nests, in the nest boxes. On 11 June 1998, we discovered the first Northern Saw-whet Owl nest, which contained a 1-year-old female brooding four young. That day, we banded the female at her nest, located at Rivière-Saint-Jean (50° 18′ N, 64° 22′ W); on 29 February 2000, the bird was recaptured in the United States at Port Elizabeth on Cape May, New Jersey (39° 18′ N, 74° 58′ W) (Patuxent Bird Banding Laboratory, Maryland). In 1999, we found three nest boxes occupied by Northern Saw-whet Owls. In one nest, egg-laying occurred in early April, and in two others it occurred at the beginning of May. On 15 December 1999, we captured a hatching-year male by using an audio lure and, on 24 June 2000, we found two partially hatched clutches, indicating that egg-laying had occurred between 22 and 26 May. No breeding attempts

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TABLE 1. Nesting records for Northern Saw-whet Owls in the Mingan Region, Quebec (1998–2003).

Year	No. eggs	No. fledged	Location	Latitude (N)	Longitude (W)
1998	≥4	2	Rivière-Saint-Jean	50°20′31″	64°26′38″
1999	≥4	4	Rivière-Saint-Jean	50°18′03″	64°21′57″
1999	6	5	Longue-Pointe-de-Mingan	50°16′24″	64°08′44″
1999	4[a]	2	Longue-Pointe-de-Mingan	50°16′25″	64°08′45″
2000	3	2	Rivière-Saint-Jean	50°18′03″	64°21′55″
2000	3	3	Magpie River	50°19′12″	64°28′07″
2001[b]	—	—	—	—	—
2002[c]	≥1	≥1	Longue-Pointe-de-Mingan	50°16′06″	64°12′49″
2002	≥1	≥1	Longue-Pointe-de-Mingan	50°15′40″	64°09′41″
2003	6	6	Rivière-Saint-Jean	50°18′03″	64°21′55″

[a] Two eggs abandoned.

[b] No nesting attempts.

[c] In 2002, four other owl nesting attempts were recorded, but species was not determined (Association Le Balbuzard, Rivière-Saint-Jean, Quebec).

were recorded in 2001. During a post-breeding check of nest boxes in 2002, we found six *Aegolius* nests, including two Northern Saw-whet Owl nests—identified by the abandoned eggs and dead nestlings inside. Finally, on 23 July 2003, one partially hatched Northern Saw-whet Owl clutch (six eggs) was recorded at Rivière-Saint-Jean, suggesting that egg-laying likely occurred 21–26 June; on 24 August, three young had fledged and three were still in the nest box. Overall, the Northern Saw-whet Owl nests we found contained 4.4 eggs ± 1.5 SE (range = 3–6, $n = 5$) and fledged 3.4 young ± 1.6 SE (range = 2–6, $n = 7$). All nest boxes were located in forested habitats within 5 km of the St. Lawrence River. The area is underlain by old marine deposits and characterized by bogs, conifer forests (balsam fir-black spruce and balsam fir-white birch), and igneous rocky hills and terraces rarely >300 m in elevation. Egg-laying dates ranged from early April to late June, indicating variable breeding conditions between years.

The discovery of a Northern Saw-whet Owl nesting population on the north shore of the St. Lawrence River extends the species' known breeding range to >50° N latitude (Fig. 1). We have no data indicating that this represents a recent expansion of the owl's range; more likely, our observations are refinements of what is known about the limits of its nor-

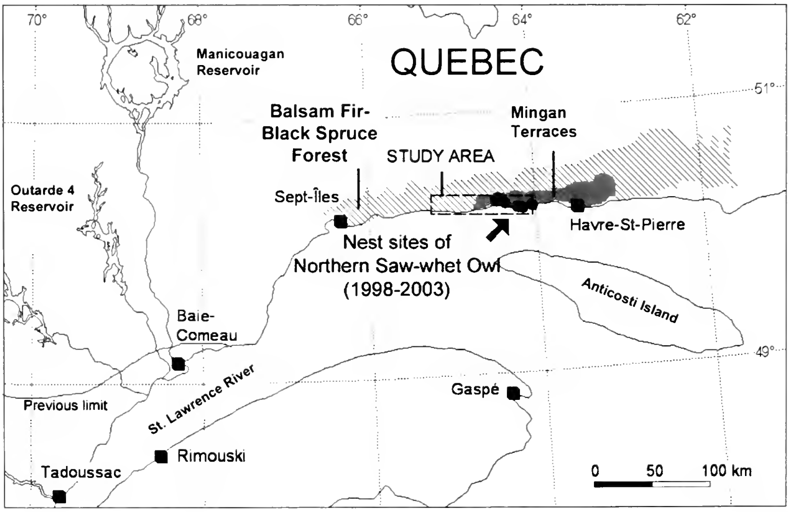

FIG. 1. Previous northern limit of known breeding range, and nest-site locations, of Northern Saw-whet Owls in the Mingan Region, north shore of the St. Lawrence River, Quebec (1998–2003).

mal range. The Mingan Terraces were thought to be inhabited primarily by Boreal Owls, although, both Boreal and Northern Saw-whet owls use coastal areas and even nest in similar habitats. Each fall, however, southern movements of Northern Saw-whet Owls are observed along the north shore of the St. Lawrence, whereas southern movements by Boreal Owls occur only about every 4 years (Observatoire d'oiseaux de Tadoussac: http://www.explos-nature.qc.ca/oot/index_f.htm).

In North America, the breeding ranges of Northern Saw-whet and Boreal owls overlap broadly in western mountain ranges, although Boreal Owls tend to occupy the higher elevations (Palmer 1986, Cannings 1993). In some years, Northern Saw-whet Owls establish territories adjacent to those of Boreal Owls at higher elevations in British Columbia (R. J. Cannings pers. comm.), and territorial overlap between the two species has been documented along the southern edge of the boreal forest in Minnesota (Lane and McKeown 1991). Clearly, the cohabitation of these closely related species in Quebec deserves further study.

ACKNOWLEDGMENTS

We thank the Canadian Wildlife Service, Ministère des Resources naturelles et de la Faune, Parc national du Saguenay, Observatoire d'oiseaux de Tadoussac, Explos-Nature, the Mingan Archipelago National Park, and the Caisse Populaire Desjardins de Mingan-Anticosti for their financial and logistical assistance and/or data. We thank M. Pierre-Alain Ravussin for his advice at the beginning of our nest-box program. We thank R. J. Cannings, J. S. Marks, B. Drolet, and an anonymous reviewer for their comments and M. Melançon for his help with the figure. We thank the volunteers that participated in the monitoring of nest boxes: S. Angel, M. Bourdon, M.-H. Lattaro, L. Lefebvre, and V. Vogel.

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The Wilson Journal of Ornithology 118(3):413–415, 2006

Carolina Wren Nest Successfully Parasitized by House Finch

Douglas R. Wood[1,3] and William A. Carter[2]

ABSTRACT.—We report the first observation of a House Finch (*Carpodacus mexicanus*) successfully parasitizing a Carolina Wren (*Thryothorus ludovicianus*) nest. On 24 May 2005, we found a Carolina Wren nest in south-central Oklahoma containing four Carolina Wren eggs and two House Finch eggs. The House Finch eggs hatched and nestlings grew rapidly. The Carolina Wren eggs hatched but the young did not survive. We observed a House Finch fledgling with the adult Carolina Wrens the day after fledging. *Received 29 August 2005, accepted 14 March 2006.*

House Finches (*Carpodacus mexicanus*) expanded their range into central Oklahoma by the 1990s (Reinking 2004). Typically,

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House Finches nest near human habitation and lay an average of four eggs; the incubation period is 13–14 days, and young fledge 11–14 days after hatching. This species has been documented as an occasional interspecific brood parasite; however, there are no records of House Finches successfully parasitizing another species (i.e., a host species fledging House Finch young; Shepardson 1915, Holland 1923, Woods 1968). Therefore, our observation of a Carolina Wren (*Thryothorus ludovicianus*) pair successfully fledging two House Finch young is noteworthy.

The Carolina Wren is a regular breeding species in south-central Oklahoma (Reinking 2004) and builds a nest of various materials in a wide variety of nest sites. Typically, Carolina Wrens lay four eggs that hatch in approximately 15 days (Haggerty and Morton 1995). Brown-headed Cowbirds (*Molothrus ater*) occasionally parasitize Carolina Wrens in Oklahoma (Bent 1948), and Carolina Wrens have successfully incubated cowbird eggs and fledged cowbird young (Grzybowski 1995, Haggerty and Morton 1995).

On 24 May 2005 at 16:15 CST, we flushed a Carolina Wren from a nest located northeast of Ada, Pontotoc County, Oklahoma (34° 49′ N, 96° 36′ W). The nest was 1.87 m above the ground, nestled between a branch and the wall of a chimney, semi-domed, and constructed of twigs, leaves, and grass. In 2003 and 2004, the same nest site was used by a pair of Carolina Wrens that were banded in 2003. The nest contained four Carolina Wren eggs (mean size = 19.5 × 15 mm) and two House Finch eggs (23 × 16 mm and 21 × 16 mm). We determined that they were House Finch eggs based on size, blue color, and maculation pattern (Baicich and Harrison 1997). One desiccated Carolina Wren egg was found just outside the nest and was not present the following day.

The House Finch eggs hatched on 3 June and two Carolina Wren eggs hatched on 6 June. By 7 June, a third Carolina Wren egg had hatched and, on 8 June, only two House Finch nestlings and one unhatched Carolina Wren egg remained in the nest. We removed the remaining unhatched wren egg and determined that it was infertile; we found no embryo in the contents. Prior to banding the nestlings, we definitively identified them as House Finches based on size, plumage, bill shape, and general morphology (Hill 1993).

We observed the adult wrens feeding insects and insect larvae to the finch nestlings. We did not observe adult House Finches feeding the nestlings, although adult finches used nearby feeders with black oil sunflower seeds. Typically, House Finch nestlings are raised on a diet composed of seeds (Beal 1907); however, our observation suggests that House Finch nestlings can be raised on a diet of primarily soft-bodied insects and insect larvae. On 13 June, both House Finch nestlings fledged and remained within 10 m of the nest. We observed the adult wrens feed the fledglings and give alarm calls when we approached. On 14 June, we observed the adult wrens foraging and feeding one House Finch fledgling 50 m from the nest site; we did not observe the House Finch fledglings after that day.

House Finches have been documented as interspecific brood parasites of Black Phoebe (*Sayornis nigricans*), Cliff Swallow (*Petrochelidon pyrrhonota*), and Hooded Oriole (*Icterus cucullatus*) (Shepardson 1915, Holland 1923); to our knowledge, however, our report is the first to document House Finch nestlings fledging from a host species' nest. Although House Finches intentionally parasitize and usurp the nests of other species, we cannot exclude the possibility that egg dumping may be an alternate explanation for our observation. Interspecific egg dumping has been documented for a variety of passerines. Wiens (1971) reported egg dumping by a Grasshopper Sparrow (*Ammodramus savannarum*) in a Savannah Sparrow (*Passerculus sandwichensis*) nest, and Sealy (1989) documented egg dumping by a House Wren (*Troglodytes aedon*) in a Yellow Warbler (*Dendroica petechia*) nest. Hamilton and Orians (1965) speculated that egg dumping is the first step towards facultative brood parasitism and, eventually, obligate brood parasitism.

ACKNOWLEDGMENTS

We thank D. W. Pogue, M. D. Duggan, and three anonymous reviewers for providing comments on this manuscript.

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The Wilson Journal of Ornithology 118(3):415–418, 2006

American Coot Parasitism on Least Bitterns

Brian D. Peer[1]

ABSTRACT.—American Coots (*Fulica americana*) are known for laying eggs in the nests of conspecifics, but there is little evidence that they regularly parasitize the nests of other species. I found 13 Least Bittern (*Ixobrychus exilis*) nests, 2 of which were parasitized by coots. These are the first records of coots parasitizing Least Bitterns, and the first records of any form of brood parasitism on Least Bitterns. Nests of Least Bitterns also were parasitized experimentally with a variety of nonmimetic eggs and 27% were rejected (n = 11 nests). This indicates that Least Bitterns may possess some egg recognition abilities. *Received 15 August 2005, accepted 21 March 2006.*

Facultative avian brood parasites build nests and raise their own young, but they also lay eggs in the nests of conspecifics (conspecific brood parasitism; CBP) and sometimes in the nests of other species (interspecific brood parasitism; IBP). CBP has been documented in at least 236 bird species (Yom-Tov 2001) and appears to be relatively common in colonial birds, waterfowl, and cavity-nesters (MacWhirter 1989, Rohwer and Freeman 1989, Yom-Tov 2001). One of the best-studied conspecific brood parasites is the American Coot (*Fulica americana*; Arnold 1987; Lyon 1993a, 1993b, 2003). CBP appears to be a relatively common reproductive strategy among coots. For example, Lyon (1993a) found that 13% of all coot eggs over a 4-year period were laid parasitically and more than 40% of nests were parasitized by conspecifics. The parasites are females with nesting territories that lay parasitically prior to laying eggs in their own nests, and floater females that are unable to acquire nesting territories of their own (Lyon 1993a).

On rare occasions, coots have been known to lay eggs in the nests of other species. To date, three host species have been recorded: Franklin's Gull, (*Larus pipixcan*; Burger and Gochfeld 1994), and Cinnamon Teal (*Anas cyanoptera*) and Redhead (*Aythya americana*) (Joyner 1973). It is unknown whether any of these cases of parasitism were successful, although coot chicks are dependent on their par-

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TABLE 1. Responses of Least Bitterns to natural and experimental brood parasitism in Warren County, Iowa, 2003–2004.

Nest	Host's clutch size when parasitized	Nesting stage when parasitized	Egg type added	Accepted or rejected
03–3	5	Incubation	Plaster cowbird egg	Rejected
03–16	5	Incubation	Least Bittern egg colored black	Accepted
03–18	6	Unknown	Two naturally laid coot eggs	Accepted?[a]
03–19	6	Incubation	Wooden egg colored black	Rejected
03–20	3	Laying	Least Bittern egg colored black	Accepted
03–22	4	Unknown	One naturally laid coot egg	Accepted
03–31	5	Laying	One coot egg placed in the nest	Accepted
03–32	6	Incubation	Wooden egg colored black	Accepted
03–34	6	Incubation	One coot egg placed in the nest	Accepted
04–49	2	Laying	One coot egg placed in the nest	Accepted
04–55	4	Incubation	Wooden egg colored black	Rejected

[a] One of two coot eggs disappeared from this nest along with two Least Bittern eggs.

ents for food and typically perish without their assistance (Brisbin et al. 2002); thus, it is unlikely that these instances of parasitism were successful (B. E. Lyon pers. comm.). I report the first records of American Coot parasitism on Least Bitterns (*Ixobrychus exilis*). I also experimentally parasitized Least Bittern nests to determine whether bitterns possess defenses, such as egg rejection, against parasitism.

METHODS

This study was conducted in a restored wetland in Warren County, Iowa, just north of Indianola (41° 4′ N, 93° 6′ W), in 2003 and 2004. The dominant vegetation consisted of cattails (*Typha* spp.) and willows (*Salix* spp.), and water depth was <1.5 m. Nests of Least Bitterns, American Coots, Pied-billed Grebes (*Podilymbus podiceps*), and passerines such as Great-tailed Grackles (*Quiscalus mexicanus*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Marsh Wrens (*Cistothorus palustris*) were monitored every 1–3 days.

I also experimentally parasitized Least Bittern nests with a variety of egg types during laying and incubation to determine their responses to parasitism. These eggs included (1) the Least Bittern's own eggs (31 × 24 mm; Baicich and Harrison 1997) colored black with permanent-ink markers to make them nonmimetic, (2) real coot eggs (49 × 34 mm; Baicich and Harrison 1997), (3) wooden eggs colored black (34 × 22 mm), and (4) plaster eggs (21 × 16 mm) made to look like those of the Brown-headed Cowbird (*Molothrus ater*; Table 1). The latter two egg types have been used in similar egg-recognition experiments (Rothstein 1975, Peer and Bollinger 1998, Peer and Sealy 2001). Only one egg type was added to each nest. Experimentally parasitized nests were checked every 1–3 days to determine the responses of Least Bitterns. Eggs were considered rejected if they were missing from the nest after it was parasitized.

RESULTS

Coots parasitized 18.2% (n = 11) of Least Bittern nests in 2003 and no nests (n = 3) in 2004. The first parasitized nest contained six bittern eggs and two coot eggs when found. Four bittern eggs hatched, and two bittern eggs and one coot egg disappeared. The second parasitized bittern nest was found containing four young bitterns and a coot egg that never hatched. Both parasitized nests were located near the water level, whereas the unparasitized bittern nests were at least 30–60 cm above the water level. Seven Pied-billed Grebe nests, 15 coot nests, and 1 unidentified duck nest also were monitored, but there was no evidence of parasitism on these nests.

The single artificial cowbird egg that was added to a bittern nest was rejected the following day, as were two of three black wooden eggs (10 and 13 days; Table 1). None of the colored bittern eggs was rejected (n = 2) and only one coot egg may have been rejected within 8 days after it was found ($n = 5$; Table 1).

DISCUSSION

These are the first reported instances of American Coot parasitism on Least Bitterns (see Gibbs et al. 1992) and the first record of any form of brood parasitism on Least Bitterns. The Least Bittern is likely an unsuitable host for the coot because the bittern's incubation period is 17–20 days (Gibbs et al. 1992) and the coot's is 23–27 days (Brisbin et al. 2002); thus, any coot eggs laid in bittern nests would not have sufficient time to develop and hatch. Indeed, two of the parasitic coot eggs did not hatch and the fate of the third egg was unclear (see discussion below). It is also unlikely that a coot would be fed properly or receive adequate parental care from a Least Bittern, in which case it would probably die if the egg did hatch (Brisbin et al. 2002).

Why would coots lay their eggs in a potentially unsuitable host's nest? It is possible that the coot eggs I observed were laid by floater females (B. E. Lyon pers. comm.), as floater females are unable to obtain their own nesting territories and presumably attempt to make the best of a bad situation by practicing CBP (Lyon 1993a). Such females may be unable to locate and successfully parasitize other coots and are forced to parasitize the nests of unsuitable hosts (e.g., bitterns). Interestingly, the two parasitized nests that I observed were very near water level—similar to the floating platform nests used by coots. The coots that parasitized the bittern nests, or other coots in the population, also may have been practicing CBP. Lyon (1993a) found that the reproductive success of floater females was only 6% of that of nesting females, and only 3.6% of parasitic eggs produced by floaters produced young. The reasons for the lower reproductive success of floaters were the anti-parasite behavior of hosts (rejected 38% of floater eggs) and the timing of laying: floaters tended to lay late in the host's nesting cycle (Lyon 1993a). CBP in general is not a very successful strategy among coots, as only 7.7% of all parasitic eggs produced young that survived (Lyon 1993b); however, territorial females can increase their reproductive success by laying eggs in the nests of neighbors. Brood reduction is common in coots; thus, by laying eggs in the nests of conspecifics, they maximize their reproductive success (Lyon 1993a).

Least Bitterns rejected some of the foreign eggs placed into their nests. One of the naturally laid coot eggs disappeared from a nest, but it is unclear whether this was due to rejection, partial predation, or the coot chick hatching and leaving the nest. Bitterns rejected two of three wooden eggs and the artificial cowbird egg. The latter may have been so small that the bitterns viewed it as debris and removed it from the nest; however, the wooden eggs were approximately the same size as the bittern eggs, indicating that bitterns may possess some recognition abilities. Bitterns did not remove any of their own, colored eggs or any coot eggs. Egg recognition in this species deserves further study.

ACKNOWLEDGMENTS

I would like to thank B. Lyon, P. Lowther, and an anonymous reviewer for helpful comments on the manuscript.

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The Wilson Journal of Ornithology 118(3):418–419, 2006

Brown-headed Cowbird's Fatal Attempt to Parasitize a Carolina Chickadee Nest

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ABSTRACT.—On 5 June 2003, a female Brown-headed Cowbird (*Molothrus ater*) was found dead in a Carolina Chickadee (*Poecile carolinensis*) cavity nest near Bucyrus in Crawford County, Ohio. The cowbird had little room in the cavity and likely could not remove itself after laying an egg. Carolina Chickadee nests are rarely parasitized by brood parasites, and the size of their cavity entrances likely limits parasitism by Brown-headed Cowbirds. This is the first known instance of a Brown-headed Cowbird mortality after laying an egg in the cavity nest of a host species. *Received 6 September 2005, accepted 21 March 2006.*

More than 220 avian species reportedly have been parasitized by Brown-headed Cowbirds (*Molothrus ater*; Lowther 1993). Whereas the Carolina Chickadee (*Poecile carolinensis*) is an uncommon host species, there are a few records of Brown-headed Cowbirds parasitizing that species (Friedmann 1938, Goertz 1977). The closely related Black-capped Chickadee (*P. atricapillus*) also has been parasitized, and individuals have been observed feeding Brown-headed Cowbird fledglings (Lowther 1983). Such observations suggest that these chickadee species are capable of raising the young of Brown-headed Cowbirds, but that some mechanism may be limiting Brown-headed Cowbirds from taking advantage of these potential host species more often. Cavity nesting seems to offer some protection from brood parasites, as cavity nesters have been found to have low levels of parasitism (Strausberger and Ashley 1997). Female Carolina Chickadees cover their eggs during the egg-laying stage (Brewer 1961), which also may offer protection against parasitism. Studies have revealed lower levels of parasitism among some host species because they reject cowbird eggs (Strausberger and Ashley 1997) or because they do not provide adequate nutrition to cowbird young (Mills 1988).

During 2003, we monitored a pair of color-banded Carolina Chickadees nesting in natural cavities in a 2.63-ha woodlot located in Crawford County, Ohio (40° 46′ N, 82° 58′ W). The landscape is dominated by agriculture, with woodlots scattered throughout the county. On 5 June 2003, we discovered a Carolina Chickadee nest cavity from which most of a dead female Brown-headed Cowbird's tail was protruding. The cowbird appeared to have died only a day or two before we found the nest and appeared cramped in the cavity. The cavity entrance dimensions were 38 mm high × 42 mm wide, similar to average dimensions previously reported for Carolina Chickadee cavity entrances (Brewer 1961, Albano 1992, Mostrom et al. 2002). The cavity was 155 mm deep, and the nest was made with grass, hair, feathers, and plant down. We did not measure the female cowbird, but her size appeared to be normal. Inspection of the nest confirmed that the cowbird had laid one egg, but we found no chickadee eggs in the nest. Given the depth of the nest cavity, we can only as-

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sume that the cowbird died after laying the egg because she had no room to move inside the cavity and remove herself after entering the nest.

The chickadees' cavity appeared to have been freshly excavated and the nest inside was intact. The cavity was located in a dead branch (130 mm in diameter at the cavity entrance, broken but still barely attached to the tree) that was hanging 1.2 m above ground, and the opening was oriented north-northeast. The nest tree was located about 22 m from the northern edge of the woodlot. Two adult chickadees were heard nearby, but if they were the original cavity occupants, it appeared they had already abandoned the nest. This was the third known nesting attempt by this pair of chickadees in 2003. The first nest was discovered on 18 April, when one of the chickadees was observed entering a cavity. On 24 April, their nest appeared to be complete and covered, suggesting they had laid at least one egg. On 28 April, the nest was gone and a few sticks were found in the cavity. A House Wren (*Troglodytes aedon*) eventually completed a nest and laid eggs in the same cavity. On 4 May, again the chickadee pair was observed building a new nest in a freshly excavated cavity. On 13 May, the nest had been removed by a House Wren and sticks were placed in the cavity. There was no indication that the chickadees had laid eggs in the nest.

The small entrances of chickadee nest cavities likely prevent most Brown-headed Cowbirds from even attempting to parasitize their nests. Pribil and Picman (1997) showed that the size of cavity entrances could limit a Brown-headed Cowbird's ability to parasitize House Wren nests. They proposed that a 38-mm-diameter hole was the smallest that a Brown-headed Cowbird could voluntarily exit; however, they had placed the cowbirds in a nesting box (12 × 10 × 20 cm), which provided enough room for the birds to orient themselves toward the exit hole. If a cowbird is cramped in a cavity—as we observed—it may not be able to turn and face the cavity opening, making it more difficult to remove itself from the cavity. One record of a parasitized Black-capped Chickadee nest indicated that the cavity entrance was larger than normal, allowing intrusion by a cowbird (Packard 1936). Whereas some cavities may permit entry by Brown-headed Cowbirds, most cowbirds may not attempt to parasitize such nests because of the difficulty in removing themselves from the nests after they have completely entered the cavities. This is the first reported instance of a Brown-headed Cowbird mortality after egg-laying in the nest of a cavity-nesting species.

ACKNOWLEDGMENTS

This observation was made during research funded by the Ohio Department of Natural Resources, Division of Wildlife, and by the Columbus Zoo and Aquarium. We also would like to thank P. E. Lowther, B. M. Strausberger, and A. M. Mostrom for their comments, which improved this manuscript.

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The Wilson Journal of Ornithology 118(3):420–422, 2006

Likely Predation of Adult Glossy Ibis by Great Black-backed Gulls

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ABSTRACT.—Great Black-backed Gulls (*Larus marinus*) are known to prey upon a wide range of bird species, particularly adults, young, and eggs of seabirds and waterfowl. Here, I provide the first account of Great Black-backed Gulls pursuing and attacking, in flight, a medium-sized wading bird, the Glossy Ibis (*Plegadis falcinellus*). I recorded two observations at Stratton Island, Maine, the northernmost breeding site for the Glossy Ibis in North America. *Received 12 September 2005, accepted 21 March 2006.*

Great Black-backed Gulls (*Larus marinus*) are well-known predators of colonial waterbirds. Many studies have attributed heavy losses of seabird and waterfowl eggs and young to this species (Hatch 1970, Mendenhall and Milne 1985, Mawhinney and Diamond 1999, Whittam and Leonard 1999, Massaro et al. 2000), particularly following human disturbance (Johnson 1938, Kury and Gochfeld 1975, Åhlund and Götmark 1989, Mikola et al. 1994). Great Black-backed Gulls have also been observed attacking and killing adult waterfowl (reviewed in Ryan 1990), seabirds (Robinson 1930; Snyder 1960; Harris 1965, 1980; Pierotti 1983; Russell and Montevecchi 1996; reviewed in Good 1998), migrating passerines (reviewed in Macdonald and Mason 1973), and even other gulls (Corkhill 1971; reviewed in Good 1998). Large birds may be seized or struck on the wing (Snyder 1960, Harris 1980, Burger and Gochfeld 1984, Ryan 1990), harassed and pursued on the water (Addy 1945, Sobkowiak 1986, Ryan 1990), or surprised on land (Robinson 1930, Snyder 1960). Here, I describe the first observation of Great Black-backed Gulls (length 71–79 cm, wingspan 152–167 cm, mass 1,300–2,000 g; Good 1998) attacking adult Glossy Ibis (*Plegadis falcinellus*), a medium-sized wading bird (length 48–66 cm, wingspan 92 cm, mass 500–800 g; Davis and Kricher 2000).

On 15 June 2005, I observed two aerial chases in which Great Black-backed Gulls pursued and struck Glossy Ibis in flight. Both events were recorded on a handheld camcorder (*Sony Handycam Vision* with 200× digital zoom) and later reviewed. All video was taken from a 6-m-high observation tower on Stratton Island (43° 31′ N, 70° 19′ W), a 12-ha National Audubon Society waterbird sanctuary located 2.4 km south of Prout's Neck, Saco Bay, Maine (see Kress 1998 and Chase 1994 for a detailed site description and history). The island supports approximately 100 breeding pairs of Glossy Ibis (C. S. Hall pers. comm.) and represents the northernmost nesting colony for this species in North America (Davis and Kricher 2000). Although gulls do not breed on Stratton Island (National Audubon Society gull control measures include nest destruction and shooting of gulls seen entering the island's tern colony), more than 400 Herring (*L. argentatus*) and Great Black-backed gulls reside on Stratton and nearby Bluff Island—an active, unmanaged gull colony less than 400 m away (CED unpubl. data).

Event 1.—At 15:30 EDT, I observed a Great Black-backed Gull adult in breeding plumage chasing an adult Glossy Ibis above the tree line of the wading bird colony. The ibis flew erratically, climbing high and then low, banking and trying to elude the gull. The aerial chase continued for about 1 min, at which point a second Great Black-backed Gull adult in breeding plumage joined in the pursuit. At 15:32, the latter gull struck the ibis with its bill, hitting it with such force that the ibis plummeted to the ground and out of view. I was unable to determine whether one or both gulls further pursued the ibis.

Event 2.—At 16:01, I again saw an adult Great Black-backed Gull pursuing an ibis in flight. At 16:06, a second adult Great Black-backed Gull again joined in the chase and

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struck the ibis 10–15 sec later, hitting it on the back near the rump and tearing off a small section of skin and feathers with its bill. The ibis tumbled out of the air and fell into the vegetation. The latter gull immediately followed the ibis into the vegetation. Although my view was partially obscured by the vegetation, it was clear that for the next 2–3 min, the gull was trying to gain control of the struggling ibis. At one point, the gull could be seen grasping the ibis' neck in its bill. At 16:07, the gull flew away, abandoning the ibis in the vegetation.

Following the gull's departure, Audubon staff and I retrieved and inspected the ibis. It was alive but appeared exhausted, with drooping wings and little reaction to approaching humans. There were no visible injuries other than the small surface wound inflicted during the chase. We placed the bird in a box and released it several hours later.

While this is the first account of Great Black-backed Gulls attacking adult Glossy Ibis, such attacks may be fairly common at this site but seldom observed. I have observed gulls feeding on fresh ibis carcasses on several occasions but never witnessed the kill. Additionally, during an annual wading bird and seabird census in late May, I found remains of 24 adult ibis. All carcasses had been cleaned of flesh and viscera, but they retained wings and sometimes the head/neck or legs, indicating gull predation (there are no mammalian predators on Stratton, and raptors seldom visit the site). Perhaps aerial pursuit is not the usual means of capture, and/or the events are easily missed due to the dense vegetation and trees favored by nesting ibis. Audubon personnel have also seen gulls occasionally take ibis fledglings from the air and noticed fledgling remains in the wading bird colony, but they have never conducted systematic observations to quantify predation rates (C. S. Hall pers. comm., S. Sanborn pers. comm.).

In contrast, Great Black-backed Gull depredation of other species nesting on Stratton (e.g., adult and duckling Common Eiders [*Somateria mollissima*] and tern [*Sterna* spp.] eggs and chicks) is frequently observed (CED unpubl. data). In the breeding seasons of 2004–2005, few (if any) ducklings survived to fledging as a result of opportunistic, group attacks by gulls (CED unpubl. data). Some attacks involved more than 20 gulls simultaneously descending on a crèche, fighting and plunge-diving to consume ducklings. Existing gull control practices to enhance tern restoration (nest destruction and shooting of tern predators) seem to have little benefit for eiders (and perhaps ibis), as predatory gulls continue to congregate in large numbers around crèching and nesting areas.

For a small ibis colony of 100 breeding pairs, the presumed number of Great Black-backed Gull kills reported here seems considerable and warrants further investigation. In a recent review, Davis and Kricher (2000) found no reports of predation on adult Glossy Ibis, though they described the Glossy Ibis as "an understudied species" and suggested that Peregrine Falcons (*Falco peregrinus*) likely take adults at some colonies. It appears, then, that this level of adult mortality is unprecedented and, if continued, could lead to colony extinction. Additional study is needed to determine whether a few "specialist" gulls prey on ibis at Stratton Island, and, if so, whether they prey on weak, sick, or otherwise unfit individuals.

ACKNOWLEDGMENTS

I thank D. M. Bird, S. W. Kress, C. S. Hall, and R. D. Titman for supporting my graduate work. Staff and volunteers of the National Audubon Society's Seabird Restoration Program provided assistance, field camp facilities, and logistical support on Stratton Island. This observation was recorded during a gull predation study funded by the Cornell Lab of Ornithology, the Garden Club of America (Frances M. Peacock Scholarship for Native Bird Habitat), and the Avian Science and Conservation Centre of McGill University. M. A. Gahbauer, M. A. Hudson, and three anonymous reviewers provided helpful comments on earlier drafts of this manuscript.

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The Wilson Journal of Ornithology 118(3):422–423, 2006

Tailless Whipscorpion (*Phrynus longipes*) Feeds on Antillean Crested Hummingbird (*Orthorhyncus cristatus*)

Jennifer L. Owen[1,3] and James C. Cokendolpher[2]

ABSTRACT.—A tailless whipscorpion (*Phrynus longipes*) was observed feeding on an Antillean Crested Hummingbird (*Orthorhyncus cristatus*) atop a large boulder on the island of Virgin Gorda in the British Virgin Islands. This is the first record of any avian species serving as prey for an amblypygid. *Received 13 June 2005, accepted 21 March 2006.*

Whip spiders (tailless whipscorpions), or amblypygids, are members of the class Arachnida, order Amblypygi. *Phrynus longipes* is the largest amblypygid on many Caribbean islands, including the U.S. and British Virgin Islands (Lazell 2005). The average body length of *P. longipes is* ~35 mm and the an-

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tenniform legs can reach an additional 34 mm (Quintero 1981). Amblypygids have no venom glands; instead, they use their sharp raptoral pedipalps (first pair of appendages) to capture prey. They are generally nocturnal and are considered mostly "sit and wait" predators, feeding on prey items found around their home territory in the caves and crevices between and under large rocks, and on trees (Weygoldt 2000). Although the diet of *P. longipes* consists primarily of arthropods, especially insects, it has been recorded to prey upon vertebrates, such as *Anolis* lizards (Weygoldt 2000) and *Eleuthrodactylus* frogs (Reagan and Waide 1996). There are no previous records of avian species serving as prey for any amblypygid.

Antillean Crested Hummingbirds (*Orthorhyncus cristatus*) are diurnal and inhabit the Lesser Antilles, including the British Virgin Islands (Lazell 2005). The main cause of mortality for hummingbirds is predation of their eggs and nestlings; predation on adult hummingbirds is relatively rare (Miller and Glass 1985). Thirteen cases of adult hummingbird predation have been documented worldwide, with only two events involving an invertebrate predator; the Chinese praying mantis (*Tenodera aridifolia*) was the predator in both cases (Miller and Glass 1985). Like amblypygids, the Chinese praying mantis is a "sit and wait" predator.

At 22:00 EST on 20 October 2004, J. Egelhoff observed an adult *P. longipes* (body ~30 mm long) feeding on an adult Antillean Crested Hummingbird (~80 mm long), 1 m above ground, atop a large boulder behind the Little Secrets Nature Gallery in Spanish Town, Virgin Gorda, British Virgin Islands (18° 26.68′ N, 64° 26.38′ W). The *P. longipes* was holding the hummingbird with its raptoral pedipalps and was feeding on the hummingbird's body; it continued to feed for 2 hr. At the time of observation, the hummingbird was no longer alive, and due to the mutilation caused by the feeding amblypygid, we were unable to obtain information on the hummingbird's weight, sex, or breeding status. The amblypygid is now part of the living exhibit at the Little Secrets Nature Gallery.

Although it is unknown how the *P. longipes* acquired its avian prey, our observation is the first record of an amblypygid feeding on a hummingbird, or any other avian species.

ACKNOWLEDGMENTS

We thank Jim Egelhoff and the Little Secrets Nature Gallery on Virgin Gorda, British Virgin Islands, for locating and photographing the predation incident, and to Dr. J. Lazell, The Conservation Agency, and the Falconwood Foundation for supporting research in the British Virgin Islands. We also thank Texas Tech University for financial support. This is manuscript T-9-1054 of the College of Agricultural Sciences and Natural Resources, Texas Tech University. We thank J. M. Wunderle and two anonymous reviewers for the helpful comments that improved this manuscript.

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The Wilson Journal of Ornithology 118(3):424–426, 2006

Polydactyly in a Vaux's Swift

Walter H. Sakai[1]

ABSTRACT.—I report on polydactyly in a Vaux's Swift (*Chaetura vauxi*). An extra, asymmetrically located toe was found on each foot of one swift. A check of 329 swifts from several museums produced no other examples of polydactyly in this species. A review of the literature and a query over the Internet, however, produced 10 other examples of polydactyly in wild birds. *Received 5 August 2005, accepted 27 February 2006.*

Polydactyly is a relatively common malformation phenomenon in vertebrates. It has been well documented in humans and domestic animals such as cats, dogs, mice, and chickens (Clark et al. 2000); however, it is an uncommon phenomenon and rarely reported in wild birds. A group of eight Vaux's Swifts (*Chaetura vauxi*, family Apodidae) was brought to me from the California Wildlife Center, an animal rehabilitation center in the Santa Monica Mountains in Malibu, California. On 29 April 2002, the swifts were found dead along Cross Creek Road (34° 02′ 35″ N, 118° 41′ 02″ W) near Malibu Creek, Malibu, Los Angeles County, California.

As I was preparing the birds as study skins and examining the swifts' pamprodactyl-type feet (Proctor and Lynch 1993), I found that seven of the birds were normal and one had an extra, asymmetrically located toe on each foot. On both feet, digit one (the hallux) was located 11 mm below the joint of the tibiotarsus and tarsometatarsus. The tarsometatarsi were 13.5 mm long. On the left foot, the extra digit was located on the tarsometatarsus 6 mm from the joint of the tibiotarsus and tarsometatarsus (Fig. 1A) and was 6 mm long. In addition, digit one and the extra toe of the left foot were joined by a webbing of tissue; thus, the nails touched. The extra digit on the right foot was located at the joint of the tibiotarsus and the tarsometatarsus (Fig. 1B) and was 10 mm long.

A survey of the literature and a query to museum bird curators and collection managers via the "AVECOL" listserve produced reports of 10 birds with polydactyly. Extra toes were reported for Mallard (*Anas platyrhynchos*; Napier 1963), Common (currently Wilson's)

FIG. 1. Left (A) and right (B) feet with extra toe of a Vaux's Swift (*Chaetura vauxi*) collected 29 April 2002 along Cross Creek Road near Malibu Creek, Malibu, Los Angeles County, California.

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Snipe (*Capella gallinago* [currently *Gallinago delicata*]; Fogarty 1969), Sooty Tern (*Sterna fuscata*; Austin 1969), Long-billed Curlew (*Numenius americanus*; Forsythe 1972), Ring-billed Gull (*Larus delawarensis*; Ryder and Chamberlain 1972), Common Nighthawk (*Chordeiles minor*; Chandler 1992), Common Loon (*Gavia immer*; R. Y. McGowan pers. comm.), Common Swift (*Apus apus*; Gory 1992), Common (currently Eurasian) Kestrel (*Falco tinnunculus*; Trinkaus et al. 1999), and Eastern Screech-Owl (*Otus* [currently *Megascops*] *asio*; Albers et al. 2001). An unconfirmed case of polydactyly in Anna's Hummingbird (*Calypte anna*) was reported from the San Francisco Bay Area, California (W. H. Baltosser pers. comm.)

I also checked Vaux's Swifts in the collections of two nearby museums: 75 specimens at the Los Angeles County Museum of Natural History (LACMNH), Los Angeles, California, and 157 specimens at the Western Foundation of Vertebrate Zoology (WFVZ), Camarillo, California, all of which were normal. The 73 Vaux's and Chimney Swifts (*Chaetura pelagica*) in the collection at Delaware Museum of Natural History, Wilmington, Delaware, also were reported as normal (J. L. Woods pers. comm.). C. M. Dardia (pers. comm.) reported that all 24 Vaux's Swifts in the collection at Cornell Museum of Vertebrates, Ithaca, New York, were normal.

The causes of polydactyly among vertebrate groups have included UV-B radiation (Blaustein et al. 1997), parasites (Johnson et al. 2001), parasites and pesticides in amphibians (Kiesecker 2002), nuclear radiation in humans (Lazjuk et al. 1998), and congenital defects in humans (Castilla et al. 1996). Extensive teratological studies have been conducted on Domestic Chicken (*Gallus domesticus*), and several breeds normally have five toes (Warren 1941, 1944). Unfortunately, the life history of the Vaux's Swift with polydactyly is unknown. The individual in question appeared healthy and its weight (12.8 g) did not differ from that of the other seven individuals (mean $= 12.67 \pm 0.62$; *Z*-test, $P = 0.71$) found with it, although it was lower than the mean (17.1 ± 1.3 SD, $n = 72$) weight of birds reported by Dunning (1984).

The Vaux's Swift specimen with polydactyly (Santa Monica College [SMC] SMC 1100) was prepared as a wet specimen, and the other seven specimens (SMC 1049, 1051, 1052, 1053, 1056, 1057, and 1058) were prepared as study skins. All eight specimens were then transferred to the LACMNH's Ornithology Collection (wet specimen: LACM 113615; skins: 112233, 112234, 112230, 11232, 11231, 11229, and 11228).

ACKNOWLEDGMENTS

I thank the various museum ornithology curators and collection managers who responded with both positive and negative reports, and for suggesting possible specimens. Thanks to L. Matsui, who brought the specimens to me from the California Wildlife Center where she volunteers. Thanks to R. A. Cobb and K. L. Garrett for suggestions on preservation of the specimen. Thanks to K. L. Garrett and R. Corado for access to the swifts at the LACMNH and the WFVZ, respectively. J. L. Woods provided information on swifts at the Delaware Museum of Natural History, and C. M. Dardia provided information on Vaux's Swifts at the Cornell Museum of Vertebrates. L. S. Hall provided useful comments. Photographs were taken by J. Smargis. I would like to thank E. L. Bull and two anonymous reviewers for their useful and helpful comments on this paper.

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The Wilson Journal of Ornithology 118(3):427–429, 2006

Once Upon a Time in American Ornithology

James Little Baillie, whose parents had emigrated from Great Britain to Canada, was born on 4 July 1904 in Toronto, Ontario. The fifth of 11 children, he went to work at the age of 13 after completing elementary school. When he was 16, Baillie began bird watching, and, just two years later in 1922, he was appointed as technical assistant for the ornithology department of the Royal Ontario Museum (ROM) of Zoology. From 1927 to 1931, he attended high school night classes, although he never earned enough credits to graduate. Nonetheless, his enthusiasm and profound knowledge of birds eventually resulted in his promotion to assistant curator of ornithology at ROM, a position in which he served for nearly 50 years.

Recognizing the value of public awareness in conservation endeavors, for 39 years Baillie wrote a weekly column, *Birdland*, for the Toronto Evening Telegram. He liked working with youth and mentored countless beginning ornithologists, including ecologist Robert MacArthur and artist Robert Bateman. Today, Ballie's conservation and public education legacies continue through the James L. Baillie Memorial Fund for Bird Research and Preservation (see http://www.bsc-eoc.org/organization/jlbmf.html), which provides funding opportunities for Canadian students interested in field studies and projects that improve our understanding and conservation of birds. In 1935, Baillie was elected a member of the American Ornithologists' Union—only the eighth Canadian to be so honored.

Above all else, however, Baillie was a dedicated museum man. He published reports of numerous museum expeditions and actively sought to enhance ROM's bird collection. In a 1970 tribute to Baillie, C. H. D. Clarke wrote, "Jim had a rare sense of the museum collection as . . . documents that would never cease yielding new information. . . . The fact that the whole history of environmental pollution in Sweden has been read from the molecular analyses of piths from the feathers of birds in the Swedish National Museum, the dates being the dates on labels, fitted precisely Jim's concept of the specimen as a storehouse of information yet undreamed of." In fact, Baillie's dedication to the museum concept drove him to what he felt was the most rewarding accomplishment of his entire career: acquiring Great Auk (*Pinguinus impennis*) and Labrador Duck (*Camptorhynchus labradorius*) specimens for the ROM. Although he was proud that the ROM already held 108 specimens of the Passenger Pigeon (*Ectopistes migratorius*)—"the largest collection of them in existence," he wrote to a friend—he was distraught that not one Canadian museum possessed a mounted specimen of the Great Auk. The other species that had once inhabited parts of Canada—the Labrador Duck—was represented in Canadian museums by only two specimens.

As Baillie searched for possible specimens of the Great Auk and Labrador Duck, he appealed to his weekly newspaper readership and his network of patrons for funding. In 1964, his resolve and efforts were finally rewarded (see Fig. 1). The reference for the quotes that follow is Anglin, L. 1987. Birder Extraordinaire: The life and legacy of James L. Baillie. Toronto Ornithological Club, Toronto, Ontario. Thanks to Lise Anglin and the book's publishers—Toronto Ornithological Club and Long Point Bird Observatory—for providing quotations and permission to quote from the book.—ALEXANDER T. CRINGAN; e-mail: alexc@lamar.colostate.edu

> On July 22 1964, [Baillie's] son-in-law drove [Ballie] to New York with Helen [Baillie's second wife] and Florence [his daughter] to negotiate the deal with Dr. R. S. Palmer of the American Museum of Natural History.
>
> On July 26, [they] made the return trip to Toronto with two more inanimate passengers aboard—one Great Auk and one Labrador Duck. Jim was nervous during the drive lest an accident might result in damage to the glass case or the birds. However there was no mishap.

FIG. 1. James L. Baillie contemplating the Great Auk specimen he procured in 1964 for the Royal Ontario Museum in Toronto. This specimen is widely believed to have been the one previously owned by John James Audubon (see pages 154–160, "Audubon's Auk, bird no. 20," *in* Fuller, E. 1999. The Great Auk. Harry N. Abrams, Inc. Publishers, New York). Anxious to see and paint a Great Auk and other sea birds of northern latitudes, John James Audubon embarked on a voyage to Labrador in summer 1833. Poor weather, however, precluded the expedition from ever reaching locations where Audubon could observe Great Auks. Thus, he had to acquire a mounted specimen from which to make his painting for *Birds of North America.* As reported by an officer of the Toronto Ornithological Club, "It is strongly suspected that the ROM's Great Auk was indeed Audubon's specimen." He went on, however, to mention at least one source that brought this belief into question: " . . . although everything collected was consistent with that specimen being Audubon's (nothing glaring disproving that possibility), the chain of ownership was not complete enough to provide 'absolute proof' of this, but it is very likely that this indeed is the case." According to Fuller (1999), when Audubon's Great Auk was restored and remounted in 1921, the renovator discovered that it was stuffed with old German newspapers, thus dispelling the prevailing notion that Audubon's auk was American in origin. Rather, the German association indicates an Icelandic origin.

Against somewhat unexpected odds, he had achieved a goal seen by many as unattainable. On 19 May 1970, just days before his death, Jim wrote from the Toronto General Hospital, "With a staff of three or four, we . . . acquired a Great Auk, a long-extinct Canadian bird previously represented in Canadian collections only by bones. The fact that the specimen turned out to be John James Audubon's very own specimen, from which he made his famous painting, was an unexpected bonus. Happily, at the same time, from the same U.S. ladies' college [Vassar], we acquired another Canadian we did not previously possess—a drake Labrador Duck. Previous Canadian-held Labrador ducks exist only in Dalhousie and McGill Universities. . . . The possession of these two treasures is an accepted criterion of the value of a museum's collection, in ornithological circles. . . . Both ours are magnificent birds in first-class condition, mounted in hermetically sealed cases."

EPILOGUE: *Pinguinus*, the Great Auk's genus name, reflects the species' widely used common name: "penguin." Although the derivation of *Pinguinus* is uncertain, possibilities include "pen-winged" or "pinioned," from the Welsh terms for white (pen) and head (gwyn), or the Latin word for fat (*penquis*). It was after Europeans discovered *Pinguinus impennis* in the northern Atlantic that explorers found members of the similar-looking—but very different—Spheniscidae family (penguins) in the Southern hemisphere (Montevecchi, W. A. and D. A. Kirk. 1996. Great Auk. Birds of North America, no. 260). Although the Great Auk inhabited much of the northern Atlantic, there is evidence that prehistoric people had extirpated the species from many parts of its original range. Climate changes also may have factored into the species' range contractions.

Human exploitation of this flightless species for its meat, eggs, oil, and down continued right up until the early 19th century, by which time the northern Atlantic "penguin" had become quite rare. Another significant blow to the population came in 1830, when an underwater volcanic eruption occurred near Iceland, causing tremors and massive waves that washed away the Island of Geirfuglaster—one of the species' last important breeding sites. The largest-known nesting colony of Great Auks, however, was found on Funk Island (historically known as Penguin Island), located off the coast of Newfoundland; in 1841, the last of Funk Island's auks was killed. In 1844, the species disappeared altogether when two Great Auks found on Eldey Island near Iceland were beaten to death and sold for use as stuffed specimens.—CYNTHIA P. MELCHER; e-mail: wjo@usgs.gov

The Wilson Journal of Ornithology 118(3):430–435, 2006

Ornithological Literature

HANDBOOK OF THE BIRDS OF THE WORLD, VOLUME 9: COTINGAS TO PIPITS AND WAGTAILS. Edited by Josep del Hoyo, Andrew Elliott, and David Christie. Lynx Edicions, Barcelona, Spain. 2004: 864 pp., 78 color plates, 440 photographs, 809 maps. ISBN: 84-87334-69-5. $245.00 (cloth).—Volume 9 in the landmark series, *Handbook of the Birds of the World,* concludes the suboscines with cotingas, manakins, tyrant flycatchers, New Zealand wrens, scrub-birds, and lyrebirds, and begins the oscines with larks, swallows, pipits, and wagtails. This volume follows the format proven in earlier volumes of the series, with a chapter for each family—lavishly illustrated with color photographs—followed by the species accounts. The chapters include discussions of the family's systematics, morphological aspects, habitats, general habits, vocalizations, foods and foraging, breeding, movements, relationship with humans, and status and conservation, and they wrap up with a general bibliography. The species accounts are illustrated with color plates that often include subspecies and both sexes. The accounts are organized by the same section headings as those in the family chapters—with the substitution of taxonomy, subspecies, and distribution for systematics, and the addition of descriptive notes.

As in previous volumes, the photographs in volume 9 are superlative: they capture courtship displays, bathing, agonistic behaviors, roosting birds, nests, recently rediscovered species, birds in their habitats, and "birds being birds." Those who see the photographs in this volume will be left with the impression that all one needs is a camera, and then magically pipits will pose for the camera while carrying insects in their bills and rare rainforest birds will display in plain view (and, of course, in good weather). Anyone who has ever tried to photograph wild birds (especially those where the subject is actually doing something) will recognize the difficulty involved in taking photographs of high technical quality with a pleasing composition. The few photographs of birds in the hand are of exceptionally rare species, making them worth a second look. The informative photo captions provide information that is not covered elsewhere in the text.

The Foreword by Richard C. Banks covers the topic of ornithological nomenclature. He begins with an overview of the history and development of ornithological nomenclature, which leads to a discussion on its state today, including the current International Code of Zoological Nomenclature. He recounts the development of the trinomial for subspecies in what was originally a binomial system, the purpose and use of a superspecies or subgenus, and the availability of names, holotypes, and syntypes. He goes on to discuss the relatively recent practice of naming new species with a photograph serving as the "type," the difficulties that this presents to nomenclaturists, and why naming new species inadvertently is problematic. The use of real life examples brings to light the difficulty of naming bird species. Banks also covers the issue of prevailing usage, which is contrary to the principle of priority. The section concludes with a summary of the number of new species described from the years 1920 to 2000, 30–56% of which were estimated to be truly new species—depending on the years considered.

Another Foreword (that somehow did not make the Contents) by John Fitzpatrick entails a formal description of a new tribe of tyrant-flycatchers. According to the volume's Introduction, John Fitzpatrick realized that one of the subdivisions he intended to recognize in the Tyrannidae had not been named formally, and he remedies this by naming the tribe, Contopini, in the volume's introductory material.

Some of the common names used in this volume were surprising. Rock Wren (*Xenicus gilviventris*) was used for a member of Acanthisittidae, which brings up the question of what future editors will call the Rock Wren (*Salpinctes obsoletus*) when they get to the volume that includes Troglodytidae. I was also intrigued to see the use of Collared Sand Martin (*Riparia riparia*) as the common name for Bank Swallow. I was familiar with the use of Sand Martin, but the modifier was new to me. The resolution of taxonomic tangles, such as that of the Yellow Wagtail (*Motacilla flava*) complex, is outside the true purpose of this work; accordingly, the editors treat Yellow Wagtail as one species, but the taxonomy section provides a good description of recent DNA work on this complex.

As in all previous volumes of this series, the References section is split into two parts: References of Scientific Descriptions and the General List of References. The former lacks the titles of publications listed but does include scientific name(s), whereas the latter includes the titles of listed publications. I am uncertain why the two were not merged and one standard citation used, but because this is Volume 9, it is likely too late for questions. Regardless, this book is highly recommended.—MARY GUSTAFSON, Rio Grande Joint Venture, Texas Parks and Wildlife Department, Mission, Texas; e-mail: mary.gustafson@tpwd.state.tx.us

A BIRDER'S GUIDE TO MICHIGAN. By Allen T. Chartier and Jerry Ziarno. American Birding Association, Colorado Springs, Colorado. 2004: 660 pp., 284 maps, 6 photographs. ISBN: 1-878788-13-2. $28.95 (paper).—In his Foreword to *A Birder's Guide to Michigan,* Allen Chartier and Jerry Ziarno's exhaustive guide to birding in the Great Lakes State, renowned bird-tour leader Jon Dunn describes his first trip to the state on a cross-country birding adventure. In June 1971, he and his four friends visited the jack-pine country near Mio to search for Kirtland's Warbler, which, as most birders know, breeds exclusively in the north-central Lower Peninsula (LP). After successfully seeing the warbler, he and his group left the following day for the eastern coast. Dunn's trip was typical of many birders' experiences with birding in Michigan—to see Kirtland's Warbler and leave a day or two later. With the publication of this book, however, more adventurous birders will decide to make Michigan the destination of longer trips to see its 31 other warbler species, as well as all the other species this unique northern state has to offer.

Four years in the making, this guide is by far the most thorough state-wide guide available for Michigan. The book includes 266 birding sites in 67 of the state's 83 counties, including all 15 counties located in the Upper Peninsula (UP). Indicative of the authors' knowledge of Michigan, they wrote or contributed to 166 of the site descriptions. Virtually all the site descriptions for the Southeastern LP section were authored exclusively by Chartier, and Ziarno wrote nearly all those included in the book for the Northeastern LP and UP sections. Forty-three other birders from across the state authored the remaining site descriptions. Also contributing their talents to this guide were the 24 birders who reviewed and checked the text and mileages, and another 12 that reviewed the bar graphs depicting each species' status in Michigan.

Visitors planning their first trip to Michigan will benefit from the introductory sections on topography, vegetation, bird habitats, and climate—now standard information included in all state birding guides recently published by the American Birding Association (ABA). A section entitled "The Michigan Birding Year" gives an overview of bird activity that one can expect in each month of a given season, supplementing the excellent status and occurrence bar graphs for Michigan's 303 annually occurring species and the list of casual and accidental bird species. In addition, the guide lists Michigan's mammals, amphibians, reptiles, butterflies, damselflies and dragonflies, and orchids and other plant species referenced in the book, and it provides weather data for selected cities. The authors also discuss Michigan's few potential hazards to birders, from the prevalent (e.g., biting insects and weather) to the least likely (e.g., black bears, moose, and massasauga rattlesnakes). Finally, the book lists contact information for Michigan tourism councils, birding-related telephone hotlines, internet chat groups, websites, festivals, and parks and conservation organizations.

The birding site descriptions are organized into six regions of the state; Southeastern LP, Northeastern LP, Northwestern LP, Southwestern LP, Eastern UP, and Western UP. Preceding each of these sections is a map illustrating the region's major birding areas and the alpha-numerical identifiers used for birding sites in that area. For instance, the regional map of the Southeastern LP indicates that the "St. Clair Marshes" is birding area #10, for which sites SE67 to SE71 are listed. After paging to the site description for SE67, the user will find a more detailed map showing the locations of all five sites in the St. Clair Marshes area. For a given site, the authors have included seasonal ratings of the site's birding quality, as well as the latitude/longitude reference and the page number and grid location where one would find that site in the Delorme Atlas. The directions for getting to site SE67—Metro Beach Metropark, one of the most popular migrant traps among Detroit-area birders—advise the reader that taking I-94 East actually entails traveling north from Detroit. This is one example of the detail and thought that went into the directions to all sites included in the book. The authors also advise visitors to call ahead for the park's hours of operation, warns that the park is popular with non-birders, and that birders should check South Beach at Metro Beach first, before the non-birders arrive.

In another location at Metro Beach—Pt. Rosa Marsh—I was surprised to learn that as many as 500 Common Loons have been tallied in one day during spring migration. The text also mentions that the bushes behind the nature center are a reliable place to find the elusive Connecticut Warbler, and that the Meadow Area should be checked for Red-headed Woodpecker, Orchard Oriole, and Yellow-breasted Chat—all uncommon in Michigan. Rarities that have made appearances here, such as Magnificent Frigatebird, Great White Heron, and Heerman's Gull, are mentioned as well.

Birding areas in the Northeast LP include groups of five to eight sites, each being close to a state highway or expressway; thus, each can be regarded as the equivalent of a "birding trail," such as those promoted in Texas or Minnesota. Tawas Point—a park at the north end of Saginaw Bay on Lake Huron—is one of the state's premier migrant traps and deserves at least one full day of birding. Mentioned by Jon Dunn as "indeed my favorite place to bird in all of North America," Tawas Point truly measures up to such high praise. As one of the few extremely fortunate birders to have been with Dunn in May 1996 to see the only White-collared Swift recorded in the Midwest, I can personally attest to the magic that can happen at Tawas Point. Now that the park's greatness is no longer a secret, Ziarno's description of this location and other nearby sites will make birding in the Tawas area obligatory for those also taking a Kirtland's Warbler tour in the nearby Mio area. The site description mentions the park's seasonal highlights, including Common Loons and diving ducks in the early spring and late fall, and nesting Piping Plovers, as well as all the best nearby places for observing up to 24 warbler species and many other passerines in a single day. It also suggests checking the pier behind the Holiday Inn for waterfowl and along Brownell Road near Tuttle Marsh to listen for Kirtland's Warbler—locations of which I was unaware.

An even more famous birding destination in Michigan—Whitefish Point Bird Observatory (WPBO) in the Eastern UP—has nine pages devoted to it. Along with an enticing list of casual and accidental sightings from "the point," the authors provide a thorough history of WPBO and what can be expected there on a seasonal basis. The site description also includes tables listing the site's mean early, late, and peak dates of migration, as well as seasonal averages and minimum and maximum counts for spring and fall waterbird counts, spring raptor counts, and owl banding conducted at this intensively studied migrant hotspot. The last weekends of April and May, when experienced Michigan birders flock to the area, are recommended as especially good birding times for first-time visitors. Traditionally, Memorial Day weekend is considered the beginning of tourist season in the UP; thus, readers are rightly warned to check on the opening and closing times of restaurants in the nearby town of Paradise to avoid the possibility of going hungry. WPBO visitors also are cautioned that, "even in Mid-May, temperatures can be low enough to require winter clothes." As one who has shivered through numerous early mornings of waterbird watching in the area, I would take this one step farther by suggesting that one bring along some winter clothing at any time of the year for birding along Lake Superior.

The Western UP, up to a 12-hour drive from Detroit, receives much less coverage from birders than the Eastern UP; thus, Michigan's county listers, and anyone else with a sense of adventure, will appreciate the guide's inclusion of 33 sites west of Luce and Mackinac counties. One of the lesser-known birding sites listed is the Garden Peninsula, which projects south into Lake Michigan towards Wisconsin's Door Peninsula. On Garden Peninsula, the State Forest campground at Portage Bay is an excellent spot for both passerines and shorebirds in the fall; however, this is not mentioned in the site description, illustrating that there are many birding spots yet to be discovered in the UP, especially the western portion. I look forward to making another Labor Day weekend trip there soon, and I'll be sure that my itinerary includes two other places described for that area—the Mead Plantation and the Nahma Marsh Trail. With the Stonington Peninsula being so close to the Garden Peninsula, I'll have to visit there as well. The guide makes Peninsula Point Park sound like an excellent migrant trap and, considering how little old-growth forest is left in the state, the hemlock stand at Squaw Creek also sounds intriguing.

At 660 pages long, this is a very thick birding guide, and it can be difficult to make it lie open. The back cover, however, extends an additional 4.5 inches for use as a bookmark. Inside the back cover is a handy state map denoting the state's birding regions and selected birding sites. On the map, sites are labeled according to the page numbers where their descriptions are located. The facing page has a map key, which lists all the birding sites and their page numbers for each of the state's six regions.

I saw only a few errors in this guide. One pertained to a birding site near where I live in Genesee County (in the Southeastern LP); the site was mislabeled as being presented on page 42 and occurring in adjoining Livingston County. After checking the text, however, I found that there was no birding site in Livingston County, and page 42 actually describes the site labeled as occurring on page 43—Gratiot-Saginaw State Game Area, located about thirty miles to the northwest of Livingston County. Clare County is misspelled on the state map on the inside back cover. I also noticed that there are two different area codes listed in the site description for Metro Beach Metropark's phone number. Noted in the guide's introduction is a request to send any comments and corrections to ABA's website for use in future editions of the guide.

In conclusion, all Michigan birders, and anyone else planning a birding trip to that state, should own a copy of *A Birder's Guide to Michigan.* There is no other guide like it for the state, and its detail and completeness are impressive. Thanks to Chartier and Ziarno for providing such a useful tool to promote more complete birding coverage of Michigan and for giving out-of-state birders such a user-friendly guide for discovering all that Michigan has to offer.—JEFF A. BUECKING, Michigan Rare Birds Committee, 1225 Dauner Rd., Fenton, Michigan; e-mail: jbuecking@juno.com

A FIELD GUIDE TO THE BIRDS OF THE GAMBIA AND SENEGAL. By Clive Barlow and Tim Wacher. Yale University Press, New Haven, Connecticut. 2006: 400 pp., 48 color plates. ISBN: 0-300-11574-1. $40.00 (paper).—This comprehensive guide has been very popular with birders for its inclusion of many tropical African birds. It was first published in 1997 in the United Kingdom by Christopher Helm, then reprinted with amendments in 1999, and now it has been released again in paperback by Yale University. It is the first field guide to the birds of Gambia and Senegal, and includes other areas of West Africa popular with birders from around the world.

Clive Barlow has lived in the Gambia area since 1985, and has become very familiar with the region's bird fauna. He presently runs birdwatching safaris and is very active with the conservation of Gambian birds through efforts in the Kiang West National Park and Tanji Bird Reserve conservation areas. Tim Wacher, a mammalian ecologist, resided in Gambia for five years, where he assembled a database of bird records from which came most of the distributional information for this book.

This 400-page guide provides full accounts of more than 600 bird species and depicts nearly all of them in the 48 color plates clustered at the forefront of this attractive volume. The end-boards depict maps of both Senegal and Gambia, and the nine-page introduction provides short, but useful, discussions on the region's geography, climate, vegetation, and major habitats. The habitat descriptions include marine, coastal, estuarine, mangrove, freshwater riverbank, and other wetland habitats, as well as farmlands and villages, hotel gardens, Guinea savanna, Sudan savanna, and dry Sahel of northern Senegal. The habitat section is followed by a short section on the Sejegambian avifauna, which boasts over 660 species, about a third of which are migrants from the Palearctic region. Additionally, there are descriptions and locator maps of the protected areas in Gambia and Senegal, a short discussion that will aid the reader in using this book, and illustrations of avian plumage topography that should be useful in understanding the keys and descriptions throughout the text.

High-quality plates are an important feature in any field guide, and the present volume meets that criterion nicely. The 48 plates, however, provide rather small images, which reduces the size of key characteristics used for identification. The plates also lack arrows pointing out key identification characteristics. Nonetheless, they are of excellent quality and will prove highly useful for anyone visiting Gambia and Senegal or surrounding areas.

Each species account includes the species' common and scientific names, relevant plate numbers, and a comprehensive section on identification. Comments on similar or confusing species are followed by remarks on flight characteristics, habits, voice, status and distribution, and reproduction, as well as when migrant species typically appear. Occasional vignettes illustrate such things as the differences in the nests of weaver birds, characteristic patterns of gull flights, and aerial song-flight displays among *Cisticola* species. Most field guides provide range maps for each species, but this guide provides none. This omission may be due to the fact that nearly one-third of the species are migratory, but range maps would have been very useful for resident species. Following the species accounts, this guide provides a listing of three conservation organizations and their membership information, a bibliography of cited references, and an index of English and scientific names that will allow those familiar with the region's avifauna to easily locate species accounts and plates.

Overall, the authors certainly should be commended for producing such a compact and badly needed field guide for Gambia and Senegal. I found it reasonably priced and a welcome resource for those planning to visit the area and enjoy its diversity and abundance of resident and migratory species.—HARLAN D. WALLEY, Department of Biology, Northern Illinois University, DeKalb; e-mail: hdw@niu.edu

BIRDS OF TROPICAL AMERICA: A WATCHER'S INTRODUCTION TO BEHAVIOR, BREEDING, AND DIVERSITY. By Steven Hilty. University of Texas Press, Austin. 2005: 312 pp., 12 black-and-white illustrations. ISBN: 0-292-70673-1. $19.95 (paper).—This title was originally published by Chapters Publishing of Shelburne, Vermont, as part of their *The Curious Naturalist* series, and then it was reprinted in 2005 by the University of Texas Press with an updated suggested reading list and epilogue. After being out of print for several years, this particularly well-written book is finally back in print and readily available to interested readers.

Steven Hilty discusses issues of tropical ornithology in a readable and engaging manner. He has organized the book in a series of twenty stand-alone essays, each of which focuses on a theme related to Neotropical birds. The essays are as varied as tropical habitats and the birds they support. Not only do they educate and entertain the reader, they provide some insight as to why tropical habitats and birds are so different from those of northern latitudes. The text is enhanced by black-and-white illustrations of tropical birds in their habitats.

Initial chapters cover avian community structure and diversity of Neotropical rain forests, biogeography of the Amazon River basin, and how the most recent Ice Age affected bird distribution, migration, and mixed-species flocks. Subsequent essays cover ant swarms and the bird species that follow them; avian coloration; fruit, frugivory, and avian dispersal of seeds; displays performed by manakins and cotingas; hummingbird foraging strategies; hummingbirds, flycatchers, vultures, and caciques that inhabit high altitudes; vocal production and sound characteristics; ecology of island specialists in the Amazon River basin; and seasonality in the tropics. I particularly enjoyed Hilty's explanations of commonly observed behaviors, including the song flight of the Blue-black Grassquit (*Volatinia jacarina*).

This book is recommended for all those interested in tropical birds and birding. It would make an interesting collection of readings for an ornithology class or a good read for your next tropical birding trip.—MARY GUSTAFSON, Rio Grande Joint Venture, Texas Parks and Wildlife Department, Mission, Texas; e-mail: mary.gustafson@tpwd.state.tx.us

THE WILSON JOURNAL OF ORNITHOLOGY

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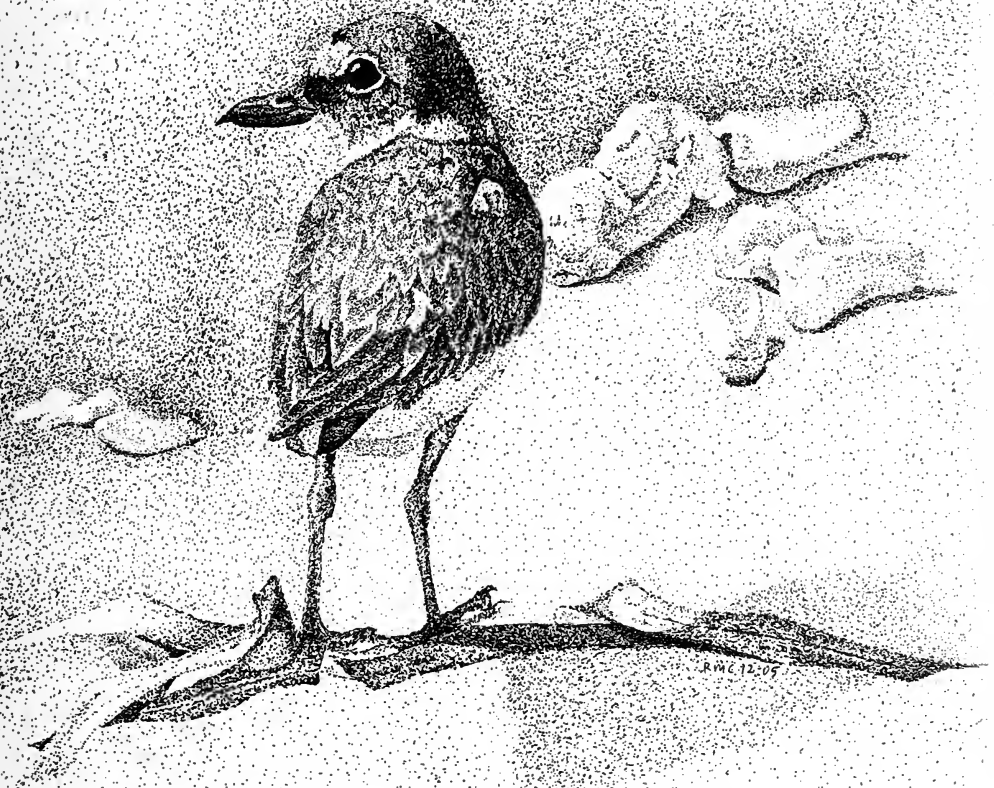

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Wilson Ornithological Society

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THE WILSON JOURNAL OF ORNITHOLOGY
(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th St., Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Blvd., Ste. 680, Waco, TX 76710.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

COVER: Wilson's Plover (*Charadrius wilsonia*). Illustration by Robin Corcoran.

FRONTISPIECE. Male American Restarts (*Setophaga ruticilla*) in second- (above) and after-second-year (below) plumage. Staicer et al. (p. 439) found that singing behavior changes with male pairing status; although a larger proportion of second-year males were unpaired than after-second-year males, the authors found no evidence that male age affected singing behavior. Original painting (gouache water color and acrylic, on paper) by Barry Kent MacKay.

The Wilson Journal
of Ornithology

Published by the Wilson Ornithological Society

VOL. 118, NO. 4 December 2006 PAGES 439–610

The Wilson Journal of Ornithology 118(4):439–451, 2006

SINGING BEHAVIOR VARIES WITH BREEDING STATUS OF AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*)

CYNTHIA A. STAICER,[1] VICTORIA INGALLS,[2,4] AND THOMAS W. SHERRY[3]

ABSTRACT.—We examined the relationship between singing behavior and breeding status in the American Redstart (*Setophaga ruticilla*) by analyzing song rates, singing mode (Repeat or Serial), and variability of song delivery in relation to the age and breeding status of 129 males in the Hubbard Brook Experimental Forest, New Hampshire. Unpaired males spent most of their time (>90%) after dawn singing in Repeat mode, whereas paired males sang sporadically, in Serial as well as Repeat mode (51% of their singing time). Males who lost their mates sang in Repeat mode at rates indistinguishable from males who had not yet obtained a mate. Overall, unpaired males sang in Repeat mode at significantly higher and less variable rates than did paired males. Although a larger proportion of second-year males were unpaired than after-second-year males, we found no evidence that age affected singing behavior.

We also assessed the effect of pairing status on male detectability in song-based monitoring surveys (e.g., point counts), and we suggest a field protocol for identifying unpaired males. Simulations of 5-min field samples, obtained from continuous samples >3 hr in duration, suggest that human listeners would be twice as likely to detect unpaired males as paired males. This result suggests that surveys based on aural detections may be biased in favor of unpaired males. In our population, >90% of males who sang >40 Repeat songs in 5 min were unpaired. Unpaired males were >3 times as likely as paired males to sing only Repeat songs in a given 5-min period. These results suggest that it may be possible to identify unpaired male American Redstarts by their high singing rates of exclusively Repeat songs. *Received 23 May 2005, accepted 30 March 2006.*

Recent interest in the song rates of male passerines has focused on the information contained in a male's singing, especially that available to females for assessing prospective mates (e.g., Hoi-Leitner et al. 1995). Many studies have found that females prefer males with a higher song rate (Gottlander 1987, Alatalo et al. 1990, Westcott 1992, Gentner and Hulse 2000, Nolan and Hill 2004), perhaps because song rate is correlated with male health (Saino et al. 1997, Smith and Moore 2003), dominance in winter flocks (Otter et al. 1997), food abundance before female arrival (Nystrom 1997), time on territory since arrival (Arvidsson and Neergaard 1991), territory quality (Radesäter and Jakobsson 1989), egg size (Smith and Moore 2003), feeding rate of older chicks by the male (Hofstad et al. 2002), and subsequent nest success (Hoi-Leitner et al. 1995). Thus, song rate appears to be an honest signal of male quality in many species.

Song rate also may be an honest signal of

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pairing status, since unpaired males typically sing more than their paired, nesting neighbors (Hayes et al. 1986, Rätti and Siikamäki 1993, Staicer 1996b, Gil et al. 1999, Amrhein et al. 2004), and males who lose their mates increase their song output (Johnson 1983, Hanski and Laurila 1993). Field experiments have shown clear effects of pairing status on male song, with an increase in singing after female removal and a decrease to pre-removal levels after female return (Krebs et al. 1981, Cuthill and Hindmarsh 1985, Staicer 1996b). If females can use these differences in singing behavior and song rates to locate unpaired males in a population, then perhaps male singing behavior contains sufficient information for humans to distinguish paired and unpaired males when monitoring songbird populations.

Typically, songbird monitoring techniques involve counts of singing males to obtain an estimate of the number of breeding pairs at a site (e.g., Ralph et al. 1995), but, if some proportion of singing males remains unpaired, these estimates may be biased and confound comparisons among sites (Rappole 1995). Males that remain unmated throughout the breeding season are not uncommon in many socially monogamous species (Breitwisch 1989, Marra and Holmes 1997). For example, in populations of the American Redstart (*Setophaga ruticilla*)—a Neotropical migrant species (Parulidae)—over half the yearling males remain unmated due to polygyny (predominantly in older males) and, possibly, to disproportionate female mortality at various times of the year (Secunda and Sherry 1991, Sherry and Holmes 1997). Moreover, in other parulids habitat fragmentation has been associated with edge- and patch-size-related excesses of unmated males (Faaborg et al. 1995, Faaborg 2002), possibly in relation to altered habitat quality or dispersal behavior. The resulting variability in male mating opportunities could influence life-history evolution. These considerations illustrate why precise determination of mating status is important, and song behavior provides a diagnostic tool (e.g., Gibbs and Faaborg 1990). Song behavior, and its interpretation, is also crucial for monitoring populations of migratory species like the American Redstart even if populations of many such species are not as imminently threatened as once thought (Faaborg 2002).

Few researchers have quantified the differences in male song rates with respect to mating status or breeding stage (e.g., Searcy et al. 1991, Nemeth 1996), nor have most researchers considered how song rate may bias population estimates (Best 1981, Hayes et al. 1986, Gibbs and Wenny 1993, McShea and Rappole 1997). If unpaired males could be distinguished from paired males by their singing behavior, then more accurate estimates of population density and habitat quality could be obtained. Although the American Redstart—a species in which many males often fail to obtain a mate—has been the subject of many studies (reviewed in Sherry and Holmes 1997), the species' song rate has not been examined.

Most of the closely related *Dendroica*, *Vermivora*, *Mniotilta*, *Parula*, and *Setophaga* species have two categories of song and they use these in different social contexts, suggesting a functional dichotomy (e.g., Ficken and Ficken 1965; Morse 1970; Kroodsma 1981; Lemon et al. 1985; Spector 1992; Staicer 1989; Weary et al. 1994; Staicer 1996a,b; Staicer et al. 1996). In Repeat mode, which is more common early in the season before pairing, males sing one song type in repetitive fashion; in Serial mode, which is more common later in the season, they alternate among two or more other song types (Lemon et al. 1985, 1987). Thus, any study involving song use in this species must consider song modes.

The delayed plumage maturation of American Redstarts has received much interest (e.g., Sherry and Holmes 1989, Lozano et al. 1996, Perreault et al. 1997). Yearling adult male American Redstarts, in their second calendar year of life (SY), are distinguishable by plumage from older males (after-second-year, ASY), making it easy to assess the effect of age on singing behavior. Most males that remain unpaired are SY (Lemon et al. 1987), but whether this can be explained by song is unclear (e.g., Morris and Lemon 1988).

The primary goal of our study was to examine differences in the singing behavior of paired and unpaired male American Redstarts with respect to song rates, regularity of song delivery, and use of song mode. In addition, we wanted to see whether (1) the breeding stage of females would influence the singing behavior of their mates and (2) whether SY versus ASY males differ with respect to singing behavior. Such information should be useful to those interested in monitoring breeding populations of American Redstarts and for stimulating similar investigations of related species.

METHODS

Study area and subjects.—Our main study area was a 140-ha stand of old, second-growth, northern hardwood forest dominated by yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) in the Hubbard Brook Experimental Forest, White Mountains, New Hampshire (Holmes and Sturges 1975). Subjects were male American Redstarts, for which breeding data were being collected as part of a long-term population study that was independent of our vocal behavior study. Males defended contiguous territories across the study area, except where eastern hemlock (*Tsuga canadensis*) and other conifers dominated. Additional observations were made in adjacent experimental, regenerating clear-cuts dominated by dense stands of paper birch (*B. papyrifera*).

Classification of breeding stages.—For paired individuals, we classified breeding stages as early association (the first hours during which a female was on territory, or briefly visiting and then moving on to another territory, up to the first day the male had pair bonded with a female), nest prospecting (female associating with the male and visiting various tree crotches), nest building, egg laying, incubation, dependence (when adults were feeding nestlings or fledglings), or lost mate (some nesting females disappeared from the territories of seven males, usually coinciding with nest predation). Information on the presence, behavior, and pairing and breeding status of males was updated every few days by another team of observers who banded birds, mapped territories, and monitored nests.

Extensive song sampling.—To document what songs birds were singing and at what rates, we recorded singing males for short periods throughout the breeding season. We attempted to record each singing male in a given area for at least 5 min. Samples were well distributed across the study area, breeding season, and hours of the morning. It took 7 days to cover the entire study area; thus, we visited different sections on consecutive observation days, repeating the cycle every 7–10 days. These extensive samples composed our main data set for examining the relationship between singing behavior and breeding stage; they did not reveal, however, whether birds were singing at a given time of day, because we only recorded males that were already singing.

A total of 129 different males were recorded over parts of three breeding seasons (23 May–19 June 1991, 13 May–26 June 1992, and 8–23 June 1993). We recorded 10 males in 2 consecutive years and one male in all 3 years. Any males that were not uniquely color-banded were identified by individual plumage; chest markings vary among males, and drawings were made for those without bands. We used sonograms to confirm the identities of males. Individuals have fairly unique repertoires and the songs of each male have unique features, making sonograms the equivalent of fingerprints. We determined the age of males (SY versus ASY) by plumage coloration (e.g., Sherry and Holmes 1997).

We made recordings between 03:33 and 15:45 EST, mostly between sunrise (~04:15) and 11:00, when songbird population surveys are typically conducted. We recorded songs on Type IV metal tape using a Marantz PMD-222 monaural cassette recorder and a Dan Gibson parabolic microphone. Using Sound-Edit software on a Macintosh computer, we made a sonogram of each song type in each recording and compared sonograms to document repertoires and verify subject identity. Once the sonograms from all recordings had been examined, Repeat- and Serial-mode songs were identified for each subject. Typical songs recorded from the study population are presented in Sherry and Holmes (1997).

Intensive song sampling.—To assess how singing behavior changed throughout the morning hours, and to provide data for modeling detectability, we studied a subset of nine (five paired, four unpaired) focal males more intensively. Males were selected for ease of study (territories accessible at dawn) and to encompass a range of breeding stages. On mornings in early- to mid-breeding season, starting with a focal male's first song at dawn, we followed each male for 210 min continuously. To facilitate maintaining contact with the focal male, we mapped his territory boundaries and studied both his song repertoire and that of his neighbors prior to the sampling date. We made sonograms of the Serial and Repeat songs of the focal male and his neighbors, and learned to recognize them by ear. For each song the focal male sang, we noted the singing mode and time the song began (measured to the nearest second with a stopwatch). The first 30 min of song was recorded on magnetic tape, and for the remaining 180 min, time of song and singing mode were tallied on data sheets.

Detectability.—We used the intensive samples to obtain an estimate of detectability for paired and unpaired males. Samples were divided into 5-min intervals; we considered a male "detected" if he sang at least one song (in either Repeat or Serial mode) during a given 5-min interval. We compared the proportion of intervals in which the 5 paired and 4 unpaired males sang. Median values were used as estimates of the detectability of paired and unpaired males.

Calculations for song rate and song cadence.—For each extensive sample, we calculated song rate (number of songs/min) and cadence (the time between the beginnings of successive songs; Reynard 1963). The time from the start of one song to the beginning of the next consecutive song was measured with a stopwatch; the median value per sample was used for all analyses. Cadence is essentially a measure of the male's singing "rhythm." To quantify the variability of this rhythm, we used the coefficient of variation (CV) of the cadence (corrected for small samples; Sokal and Rohlf 1995) expressed as a percentage, and hereafter referred to as cadence CV; a higher cadence CV indicates a more irregular delivery of songs. Whereas song rate and cadence should be negatively correlated (i.e., as song rate increases, time between songs necessarily decreases), song rate and cadence CV need not be. Additional information associated with each sample included sample duration, date and time of day, and the male's identity, age, pairing status (paired or unpaired), breeding stage (if paired), and singing mode (Repeat or Serial).

Statistical analyses.—We used nonparametric tests to determine whether pairing status, breeding stage, or time of day affected song rate or cadence CV. Data were not normally distributed and sample sizes for some groups were small, so we report medians instead of means as a measure of central tendency. Multiple samples of the same male were averaged so that each male contributed a single datum to a given group. We used Mann-Whitney *U*-tests to compare two groups of males, and all tests were two-tailed unless otherwise noted. To determine the significance of Mann-Whitney *U*-tests involving multiple comparisons, we used a sequential Bonferroni test (k comparisons by the Dunn-Sidak method) and an experiment-wise $\alpha = 0.05$ (Sokal and Rohlf 1995). We report the significance level of each test; if the Bonferroni revealed significance, we also report the Bonferroni-adjusted critical value (P_{adj}). We also calculated Spearman's rank correlations to examine the relationship between song rate and cadence CV.

RESULTS

Song modes.—The total singing time captured in our 514 samples of 129 males was 27.5 hr (median sample duration = 3.2 min). In few samples (<2%), males switched singing modes; for these, we separated the Serial song bouts from the Repeat bouts before analysis.

The dawn chorus was a period of intense singing of Serial-mode songs. Males sang in Serial mode at greater rates at dawn (14.4 songs/min, $n = 17$ males) than they did later in the day (10.3 songs/min; $n = 76$ males; Mann-Whitney *U*-test: $P < 0.001$). For a subset of eight paired males, we recorded Serial mode sequences during their dawn singing bouts as well as during later morning bouts on the same day. These males sang in Serial mode at higher rates at dawn (15.3 songs/min) than they did later in the morning (9.7 songs/min; one-tailed Wilcoxon Matched Pairs test: $P = 0.006$). Because of the robust difference between dawn and daytime song rates, subsequent analyses include only recordings obtained after sunrise (i.e., daytime songs).

Post-sunrise use of song modes varied with pairing status and nesting stage. When multiple samples from the same male in the same breeding stage were averaged, Repeat mode comprised 68% of the 225 resulting samples. Unpaired males sang in Repeat mode in 91%

of 69 samples and males who lost their mate sang in Repeat in 100% of 7 samples. In the early association stage, males sang in Repeat mode in 93% of 15 samples and in 100% of 7 samples during the nest prospecting stage. Once males were nesting, their use of Repeat mode declined. Paired males sang in Repeat mode in 51% of 71 samples during the nest-building period, 54% of 13 samples during the egg-laying period, 36% of 31 samples during the incubation period, and 67% of 12 samples during the dependence period. Overall, use of song mode after sunrise was dependent on pairing status: paired males sang in Repeat mode in only 51% of 134 samples compared to unpaired males or males who had lost their mates; these males sang in repeat mode in 92% of 76 samples (Chi-square test of independence: $\chi^2 = 26.95$, df = 1, $P < 0.001$).

After dawn song rates and cadence CV.—Unpaired males sang in Repeat mode at significantly higher rates (8.0 songs/min, $n = 68$ males) than did paired males (6.3 songs/min, $n = 82$ males; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.001$, $P_{adj} = 0.013$; Fig. 1A). Unpaired males also sang in Repeat mode with a significantly less variable cadence (cadence CV = 25.3%) than did paired males (37.8%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.001$, $P_{adj} = 0.013$; Fig. 1B).

Only 6 (8.7%) of the unpaired males we recorded sang in Serial mode after dawn, and they did so only on 1 day of observation for a brief period (median duration of recording = 1.0 min) in the first few days after arrival. Their Serial song rates were not significantly different (11.6 songs/min) than those of paired males (10.1 songs/min, $n = 69$ males; Mann-Whitney *U*-test: $P = 0.82$; Fig. 1A). Furthermore, when unpaired males sang in serial mode after sunrise, their cadence CV was similar to that of paired males (Mann-Whitney *U*-test: $P = 0.61$; Fig. 1B).

Overall, males sang in Serial mode at significantly higher rates than they sang in Repeat mode, regardless of pairing status (Mann-Whitney *U*-test and Bonferroni adjustment for paired males: $P = 0.010$, $P_{adj} = 0.017$; for unpaired males: $P = 0.017$, $P_{adj} = 0.025$). Paired males sang in Serial mode with a lower cadence CV (29.0%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.012$, $P_{adj} =$

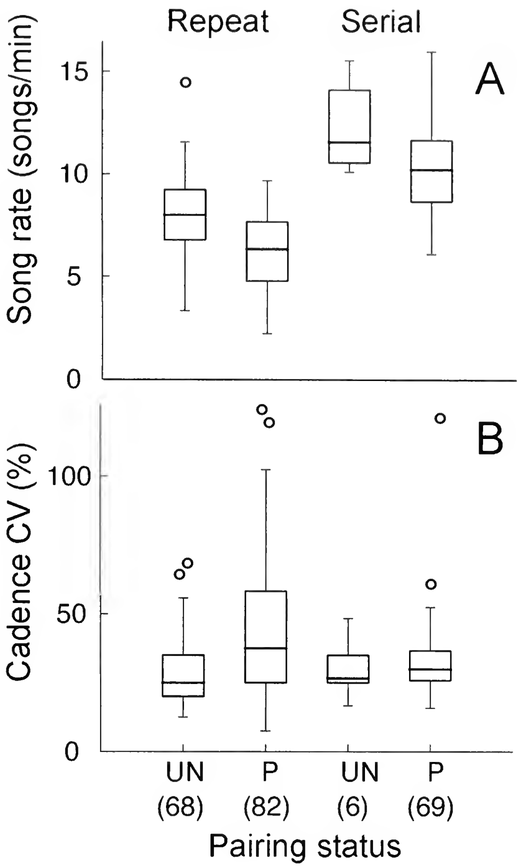

FIG. 1. Effects of pairing status on (A) song rate and (B) variability of song delivery (cadence CV) for male American Redstarts at Hubbard Brook Experimental Forest, New Hampshire, 1991–1993. Repeat and Serial mode sequences of paired (P) and unpaired (UN) males were recorded after 04:15 EST. Higher cadence CV values indicate more variation in timing between songs. Sample sizes in parentheses indicate number of males; for a given status, multiple samples per male were averaged, so that each male contributed a single datum. Samples from males in the early association stage (early stages of pairing or unpaired males who were visited briefly by unpaired females) could not be classified unambiguously and were excluded from this analysis. Box plots show the medians (horizontal center lines), interquartile ranges (between the upper and lower edges of the box, within which 50% of the data lie), values within ±1.5 times the interquartile range (bars extending from box edges), and outliers (open circles). Unpaired males sang in Repeat mode significantly faster and with a more regular cadence than paired males (Mann-Whitney *U*-test; Bonferroni adjustment for both comparisons: $P_{adj} = 0.013$). See text for additional results and statistical tests.

0.017) than they sang in Repeat mode (Fig. 1B). Unpaired males sang in Repeat mode with a similar cadence CV as did paired males singing in Serial mode (CV = 27.0%; Mann-Whitney *U*-test: $P = 0.36$).

Cadence CV was negatively correlated with song rate for combined Repeat- and Serial-mode samples (Spearman's rank correlation: $r = -0.41$, $n = 219$, $P < 0.001$). Results were similar for Serial mode when samples were analyzed separately ($r = -0.46$, $n = 75$, $P < 0.001$). For Repeat-mode samples, the negative correlation between cadence CV and song rate was strong for paired males ($r = -0.61$, $n = 76$, $P < 0.001$) and weak for unpaired males ($r = -0.24$, $n = 68$, $P = 0.050$); thus, unpaired males sang in Repeat mode with a more regular rhythm than paired males, regardless of song rate.

Rates of Repeat mode song also changed with breeding stage (Fig. 2A). Males who lost their mate sang at rates similar to those who had not yet paired (8.3 versus 8.0 songs/min; Mann-Whitney *U*-test: $P = 0.90$). Males sang at greater rates before pairing than did males whose mates were nest prospecting (5.0 songs/min; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.006$, $P_{adj} = 0.010$), nest building (6.6 songs/min; $P = 0.001$, $P_{adj} = 0.007$), incubating (6.1 songs/min; $P = 0.009$, $P_{adj} = 0.013$), or feeding dependent young (4.2 songs/min; $P = 0.002$, $P_{adj} = 0.009$). Repeat-song rates of unpaired males did not differ significantly from those of males in early stages of pairing (early association stage, 6.5 songs/min, $P = 0.16$), or in the egg-laying stage (6.9 songs/min; $P = 0.11$; Mann-Whitney *U*-tests).

Cadence CV of Repeat songs also changed with breeding stage (Fig. 2B). Again, the cadence CV of males who lost their mates (22.5%) was similar to that of males who had not yet paired (25.1%; Mann-Whitney *U*-test: $P = 0.79$). Before pairing, males sang with a significantly more regular rhythm than did males who were beginning to associate with a female (37.0%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.008$, $P_{adj} = 0.013$) or paired males whose mates were nest prospecting (46.3%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.001$, $P_{adj} = 0.007$), nest building (38.7%; $P = 0.001$, $P_{adj} = 0.009$), or feeding dependent young (68.5%; $P = 0.002$; $P_{adj} = 0.010$). Cadence CV of unpaired males did not differ from that of males whose mates were in the egg-laying stage (CV = 22.4%; Mann-Whitney *U*-test: $P = 0.88$) or incubating (35.9%; $P = 0.09$). Thus, although song rates of unpaired males and males in the early association stage did not differ, the latter sang with a less regular rhythm. Conversely, although song rates of unpaired males were significantly greater than those of paired males whose mates were incubating, both groups sang with a similarly regular rhythm.

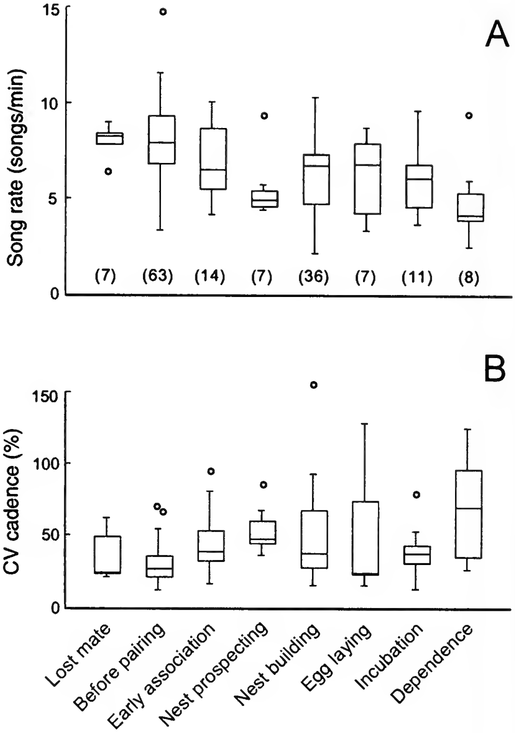

FIG. 2. Effects of breeding stage on (A) song rate and (B) variability of song delivery (cadence CV) for Repeat-mode sequences for male American Redstarts at Hubbard Brook Experimental Forest, New Hampshire, 1991–1993. Breeding stage: lost mate, before pairing, early association, nest prospecting, nest building, egg laying, incubation, and dependence (feeding nestlings or fledglings). Sample sizes in parentheses indicate number of males; often a given male contributed data to more than one stage, but within each stage, all data were independent (i.e., multiple samples per male were averaged to obtain a single datum). See text for explanations of statistical tests and the Figure 1 caption for an explanation of the box plots.

Age and song rate.—We found no significant age effects on song rate (SY versus ASY males). Unpaired SY and ASY males sang in Repeat mode at similar rates (8.6 versus 8.0 songs/min, $n = 32$ versus $n = 28$, respectively; Mann-Whitney U-test: $P = 0.24$). Paired SY and ASY males also sang in Repeat mode at similar rates (4.9 versus 5.7 songs/min, $n = 17$ versus 49, respectively; Mann-Whitney U-test: $P = 0.10$). Only 3 of the 36 unpaired SY males that we observed sang in Serial mode after the dawn bout. For paired SY and ASY males singing in Serial mode, song rates were similar (10.6 and 10.2 songs/min, $n = 11$ and 43, respectively; Mann-Whitney U-test: $P = 0.76$). Thus, song rate was not affected by male age, regardless of pairing status. The similarity in singing behaviors of SY and ASY males can be seen in the 3.5-hr samples of the nine focal males (Fig. 3).

Temporal patterns in song activity and pairing status.—Obvious differences between paired and unpaired males with regard to their singing behaviors are illustrated by 3.5-hr song counts for the nine intensively sampled males (Fig. 3). Typical of breeding males, the five paired males (Fig. 3A) sang a large number of Serial mode songs at rapid rates during their dawn bouts. Around sunrise, however, paired males usually stopped singing and for the rest of the morning sang sporadic, but typically distinct (not mixed), bouts of Repeat- or Serial-mode songs. During the incubation stage, some males (e.g., 10 June; Fig. 3A) sang little on their territory after their dawn bouts, whereas others (e.g., 16 June; Fig. 3A) sang during most of the 5-min periods after sunrise. Temporal patterns in Serial- and Repeat-mode song activity were similar for the five paired males (two SY and three ASY males).

In contrast, the four males who lacked established pair bonds (Fig. 3B) sang only in Repeat mode after sunrise, and did so more frequently and at higher rates than paired males. A male's time on territory rather than date or pairing status seemed to influence whether he sang Serial mode in the dawn chorus. The two unpaired males that did not sing in serial mode during a dawn bout, but sang only in Repeat mode before 04:00, were late arrivals in the study area (28 May and 10 June; Fig. 3B). Although these SY and ASY males were observed at different times of season, both had been singing for only a few days on territories that were adjacent to contiguous clusters of established territories. The other two unpaired males (13 June and 15 June; Fig. 3B), which had defended territories within a contiguous cluster of ASY males for ≥10 days by the time they were recorded, sang dawn Serial bouts like those of their paired neighbors but then switched at sunrise to Repeat mode and steadily sang in that mode through the morning. The male who attracted a mate during the observation period (13 June; Fig. 3B) sang only in Repeat mode but at a rate that decreased through the morning. On the previous days, no female was present; after the sample date, he remained paired and commenced nesting. The male who lost his mate after her nest was depredated (15 June; Fig. 3A) sang only in Repeat mode after sunrise, but at a slightly lower rate and with less regularity than did the males who had not yet paired.

Confounding factors.—To test whether time of day or time of season influenced Repeat-song rates, we calculated Spearman's rank correlation coefficients. Song rates of unpaired males were negatively correlated with time of day ($n = 70$, $r = -0.350$, $P = 0.010$). For paired males, however, there was no significant relationship between song rate and time of day ($n = 54$, $r = -0.10$) or time of season ($n = 54$, $r = -0.05$), and, for unpaired males, there was no correlation between song rate and time of season ($n = 70$, $r = -0.12$; all $P > 0.10$).

Sampling duration was another potentially confounding factor. Although Repeat-song rates of paired and unpaired males differed significantly, data for the two groups did overlap to some extent (Fig. 1). Overlap between paired and unpaired males, however, decreased as sample duration increased (Fig. 4). In samples lasting ≥5 min, Repeat song rates of paired and unpaired males overlapped little. In samples of ≥5-min duration, 82% of 27 unpaired males, but only 7% of paired males, sang ≥8 Repeat songs/min. In samples of 10- to 15-min duration, the median for the first 5 min was similar to the median for the entire sample.

Detectability.—Data for the nine intensively sampled males (Fig. 3) were split into 5-min intervals and each was examined for occurrence of song. Only intervals after the dawn chorus were used (median = 37, range = 35–

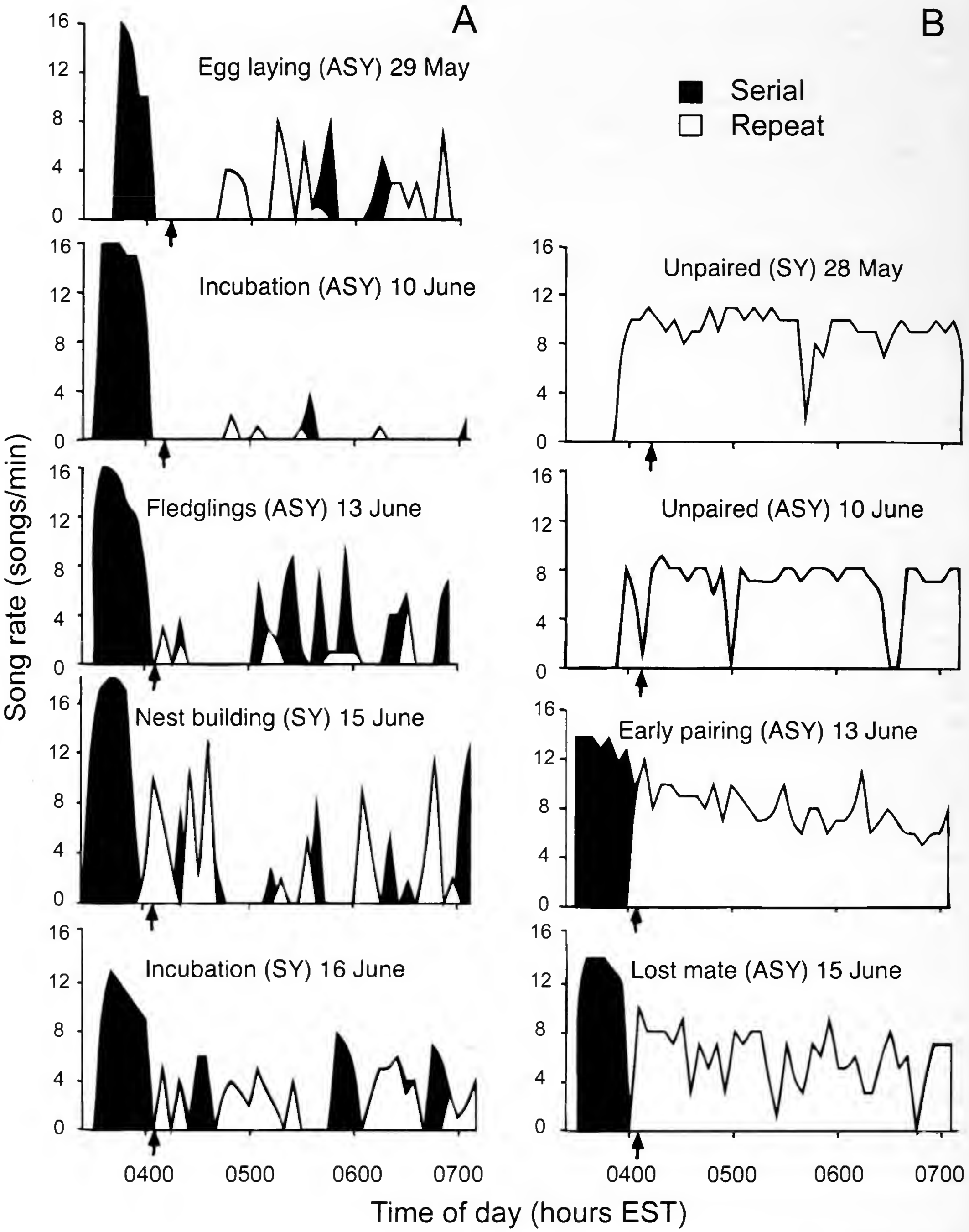

FIG. 3. Singing activity of nine American Redstart males in various breeding stages at Hubbard Brook Experimental Forest, New Hampshire, 1992–1993. SY = yearlings, ASY = older adults. Areas under curves show median number of Serial (black) and Repeat (white) songs that the subject sang per minute for each 5-min period, from his first songs at dawn until 3 hr after sunrise. Sunrise varied from 04:10 (28 May) to 04:05 EST (15 June), as indicated by arrows on the x-axis. Subjects were (A) five paired males and (B) two unpaired males within a few days of territory establishment, one male who first attracted a mate during the observation period, and one male whose mate had disappeared when her nest was depredated. Note the larger output of Repeat-mode songs from males who lacked an established pair bond (B).

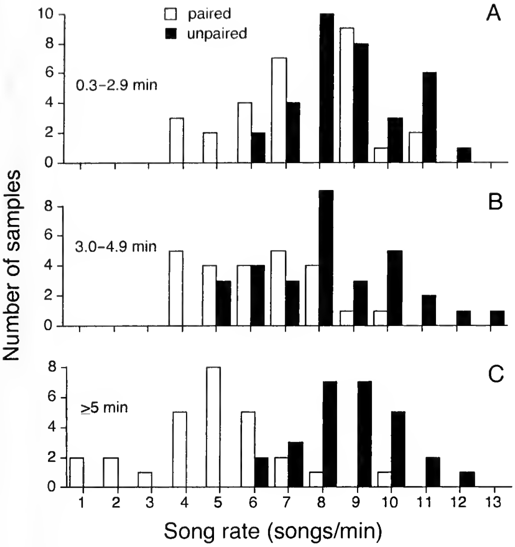

FIG. 4. Repeat-song rates of paired versus unpaired male American Redstarts using samples of three durations at Hubbard Brook Experimental Forest, New Hampshire, 1991–1993. For each duration, a given male was entered into the analysis only once. (A) Samples of short duration (0.3–2.9 min) for 37 paired and 34 unpaired males. (B) Samples of medium duration (3.0–4.9 min) for 24 paired and 31 unpaired males. (C) Samples of long duration (5–15 min) for 27 paired and 27 unpaired males. Note that as sample duration increased, the amount of overlap between the two samples decreased.

38 intervals per male). Unpaired males (n = 4) sang in 99% (median; range = 92–100%) of the 5-min intervals, whereas paired males (n = 5) sang in only 49% (median; range = 16–74%) of the 5-min intervals. Detectability was defined as the proportion of 5-min intervals in which a bird sang one or more songs. Detectability of unpaired males (0.99) was significantly greater than the detectability of paired males (0.49; Mann-Whitney U-test: P = 0.014).

DISCUSSION

Singing behavior and breeding status.—We identified three ways in which the singing behavior of unpaired male American Redstarts differed significantly from that of paired males: (1) after sunrise, unpaired males sang in Repeat mode almost exclusively, whereas paired males sang in both modes; (2) unpaired males sang Repeat songs at a significantly faster rate than did paired males; and (3) unpaired males sang with a more regular cadence than did paired males. We also documented variation in song rates and regularity of cadence in relation to breeding stage of paired males.

After the dawn bout ended, use of Serial mode varied with pairing status and breeding stage. In almost all cases in which we heard Serial mode after dawn, it was delivered by a paired male. Use of Serial mode after dawn may reflect the presence of nests or young (see also Ficken and Ficken 1965, Lemon et al. 1985), and males seem to have the greatest propensity to use Serial mode (or the equivalent song category in other species) when their mates are incubating (this study; Staicer 1989, 1996b; but see Lemon et al. 1987).

Breeding stage also affected Repeat-song rates and cadence. As males began to pair, they continued singing primarily in Repeat mode, but cadence became more irregular. Lowest rates of singing in Repeat mode were found in males whose mates were building nests and males who were feeding nestlings or fledglings. Slower song rates and more irregular cadences have been associated with the activities of foraging and associating with females (e.g., Nolan 1978, Gil et al. 1999). Although we had relatively few song samples from the egg-laying stage, these males sometimes sang for brief periods at rates that overlapped those of unpaired males. Our males, however, were silent while following their mates; thus, we found no evidence that song functions to guard females during their fertile period (see also Titus et al. 1997). Males sang in Repeat mode least often when their mates were incubating, a pattern shared with other parulid species (Staicer 1989, 1996b; but see Lemon et al. 1987).

Time of season did not appear to alter these singing patterns. Pairing and nesting were asynchronous in our population due to different arrival times of males and high rates of nest predation, after which females sometimes disappeared or, rarely, changed mates. Thus, at any given time, neighboring males often were in different breeding stages. Males who lost their mates sang at high rates, similar to males before they were paired. This change in behavior has been noted for other wood-warblers (Nolan 1978, Kroodsma et al. 1989, Spector 1991, Staicer 1996b) and other groups of passerines (e.g., Wasserman 1977, Krebs et al. 1981).

To determine whether females select males with higher song rates, additional data, such as pairing order, male condition or quality, and territory quality must be obtained (e.g., Hoi-Leitner et al. 1995, Nystrom 1997). If vocal behavior is important in mate choice, however, we might expect to find differences between SY and ASY male American Redstarts. We found no evidence that age affects song rate or singing mode when pairing status was taken into account. Although age influences competitive ability (Sherry and Holmes 1989), pairing success (Morris and Lemon 1988), and extra-pair fertilizations (Perreault et al. 1997), these effects appear to be caused by the later arrival of yearlings rather than age effects on song behavior (Lozano et al. 1996; TWS unpubl. data).

Implications for population monitoring.— Few researchers have examined the possibility of distinguishing unpaired from paired males based on their song behaviors, despite the potential utility of such information in population monitoring. Our results suggest that a considerable amount of potentially useful information is available in the singing behavior of male American Redstarts. Unpaired males sang at steadier and higher rates, took fewer and shorter breaks from singing (usually ≤5 min), and typically sang only in Repeat mode after sunrise. After the dawn chorus, Serial mode was heard from paired males almost exclusively; typically, if a male sang in Serial mode, he was paired. A trained ear can easily distinguish Repeat from Serial mode. In Repeat mode, the same song type is repeated, whereas in Serial mode, males rapidly alternate between 2–5 noticeably different songs (e.g., Lemon et al. 1985).

In 5-min samples from a large number of males, the Repeat-song rates of unpaired and paired males overlapped little. We further assessed the information available in a 5-min sample by combining estimates of detectability (whether a male sang any songs in the 5-min period) with the likelihood that a male already detected was singing in Repeat mode. The probability that a singing male sang in Repeat instead of Serial mode differed for paired (0.51) versus unpaired (0.92) males. Detectability also differed for paired (0.49) and unpaired (0.99) males. The chances that a paired male would sing any Repeat songs within a 5-min interval was only 0.25 (0.51 × 0.49). In contrast, the chances that an unpaired male would sing in Repeat mode within a 5-min period was 0.91 (0.92 × 0.99). Thus, unpaired males were 3.6 times (0.91/0.25) more likely to sing in Repeat mode in a given interval than were paired males.

Our results suggest that unpaired males should be distinguishable from paired males in field surveys. When conducting point counts, an observer could listen to a singing male for a prescribed period of time, note whether he is repeating the same song (Repeat mode) or alternating songs (Serial mode), and tally the number of Repeat songs he sings per minute or the number of seconds that lapse between successive songs. In our study population, a critical song rate of 8.0 Repeat songs per min for 5 min (>40 songs total) would identify the male as "unpaired" with reasonable certainty. If a male sang in Serial mode during the same 5-min period, we could be reasonably certain that he was "paired."

The presence of unpaired males can confound estimates of the numbers of breeding birds. Unpaired males are common in American Redstart populations, with yearlings forming the bulk of males that are unsuccessful in obtaining mates (Sherry and Holmes 1997). Our data show that unpaired males are about twice as likely as paired males to be detected during brief listening intervals (e.g., 5 min). Similar results have been reported for several other species (Best 1981, Mayfield 1981, Gibbs and Wenny 1993).

The utility of such a protocol for detection of trends over time (or space) is demonstrated in the following hypothetical case. Assume that 100 males are within earshot, 5-min counts are conducted, and the listener always detects and correctly identifies a given song. If, in year 1 (or habitat A), all males are paired, only 49 males would be reported (using our calculated detection probability = 0.49). If only half of the 100 total males are paired in year 2 (or habitat B), then only ~25 (50 × 0.49) of the paired males would be detected while nearly all of the unpaired males (50) would be detected (using our calculated detection probability = 0.99), for a total of ~75 males reported. Based on the data, we would erroneously conclude that the population increased from year 1 to year 2 (or that the population in habitat B was larger than that in habitat A).

Correcting the data by removing unpaired males from the total detected and taking into account the lower detectability of paired males provides a very different picture of population status. Assume we use the protocol whereby, for a given male, detecting ≥40 songs per 5-min sample indicates that he is unpaired, and 10% of males are misclassified (based on the type of overlap illustrated in Fig. 4C). In year 1 (or in habitat A), we would correctly classify 44 (and misclassify 5) of the 49 paired males that were detected, and then double this number for a total estimate of 88 breeding pairs. In year 2 (or in habitat B), 22 of the 25 paired males detected would be correctly classified as paired and 5 of the detected unpaired males would be misclassified as paired, for a total of 27 paired males (22 + 5) detected. Correcting for the 0.49 detection rate of paired males yields a total estimate of ~54 pairs in year 2 (or in habitat B). Both corrected estimates fall within 10% of the actual number of breeding pairs. The large population decline from year 1 to year 2 becomes visible (or the lower population density in habitat B becomes obvious). Thus, the information about the relationship between pairing status and song rates in this species, and perhaps others, can potentially be used to obtain more accurate population estimates.

ACKNOWLEDGMENTS

This study was supported by a Carnes Award and an American Ornithologists' Union Research Grant to CAS and VI, and National Science Foundation Grants to Dartmouth College (R. T. Holmes) and Tulane University (TWS). Marist College provided three Summer Research Grants and a sabbatical leave (VI). Recording and analysis equipment and software were provided by Marist College (including equipment loans from the School of Communication and the Arts), and by Dalhousie University (research development grant to CAS). We thank the U.S. Department of Agriculture Forest Service for allowing us to conduct the study at the Hubbard Brook Experimental Forest. We also thank the many field assistants (including J. Clark, J. Crews, M. L. Deinlein, R. Heins, J. I. Lovette, P. P. Marra, and T. S. Wilkinson) for monitoring nests, G. Drake for technical assistance, and R. T. Holmes for logistical support and encouragement at Hubbard Brook. We wish to extend special thanks to A. Molloy, who encouraged this research and helped us obtain the equipment necessary to process and analyze sonograms. We also thank J. P. Saunders and M. G. Tannenbaum for proofreading the manuscript. D. Nelson, J. C. Nordby, D. A. Spector, and four anonymous reviewers provided useful comments on previous drafts.

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The Wilson Journal of Ornithology 118(4):452–460, 2006

INVESTMENT IN NEST DEFENSE BY NORTHERN FLICKERS: EFFECTS OF AGE AND SEX

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ABSTRACT.—At early breeding stages, male woodpeckers invest heavily in nest construction and defense, but parental contributions to brood defense among Picidae are not well known. We studied the Northern Flicker (*Colaptes auratus*) to determine whether sex, age, brood size, body size, or body condition influenced defense behavior. When presented with a model predator (red squirrel, *Tamiasciurus hudsonicus*) during the brood-rearing period, parents exhibited a range of behaviors, such as blocking the nest hole, diving at the model, and striking the model; however, defense scores did not differ between males and females aged 1, 2, or 3+ years old. Although we predicted that defense level would be positively correlated with brood size, we found no such relationship. Adult body size and condition also were not related to defense intensity. We conclude that the sexes may exhibit similar levels of defense because they have similar apparent annual survival rates and males are only slightly larger than females. If flickers optimize clutch size according to the number of offspring they can rear, then there may be no relationship between defense and brood size. *Received 20 September 2005, accepted 6 July 2006.*

Although nest defense may deter predators, it may place the parent bird at considerable risk while requiring significant energy expenditure (Blancher and Roberstson 1982, Nealen and Breitwisch 1997, Olendorf and Robinson 2000). For many birds, the intensity of nest defense may increase (1) as the breeding season and reproductive value of the brood increases (see Montgomerie and Weatherhead 1988 for a review), (2) as the potential for renesting declines (Andersson et al. 1980), and (3) with clutch or brood size (Olendorf and Robinson 2000). Moreover, the intensity of defense may depend on the sex of the parent defending the nest (Breitwisch 1988, Sproat and Ritchison 1993, Nealen and Breitwisch 1997).

Age may be correlated with the level of nest defense for several reasons, but this has rarely been tested (Veen et al. 2000). Older birds have a lower probability of future reproduction; thus, they should invest more in broods than younger individuals (Hatch 1997). In addition, it is often difficult to separate the effects of age from experience with predators because they are often directly correlated. Similar to older birds, birds with more experience also may be willing to defend their nests more aggressively (Veen et al. 2000).

Levels of defense also may vary between the sexes (e.g., Breitwisch 1988, Sproat and Ritchison 1993, Tryjanowski and Golawski 2004) because of intersexual differences in future survival and body size (Montgomerie and Weatherhead 1988). The sex with the lower survival rate and, consequently, the lower probability of future breeding, should defend broods more vigorously than its partner (Montgomerie and Weatherhead 1988). Mortality is usually female biased in many bird species, likely as a result of high reproductive costs (Promislow et al. 1992). Generally, the larger sex defends the nest more aggressively, perhaps because the risk of injury is lower or because larger birds are able to mount strong attacks (Tryjanowski and Golawski 2004). Because healthy birds may have relatively greater energy reserves, they may take more risks when defending their nests than birds in poorer condition (Martin and Horn 1993). For example, females may be in poorer condition after incubation and defend the nest less aggressively than the male (Sproat and Ritchison 1993).

Cavity nesters may rely more on the inaccessible or cryptic nature of their nest than on active nest defense (Weidinger 2002); however, there have been few studies of woodpecker behavioral responses to predators at the nest site. Wiebe (2004) examined responses of the Northern Flicker (*Colaptes auratus*)

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to the European Starling (*Sturnus vulgaris*)—a kleptoparasite of cavity nests (Kappes 1997)—but found no sex- or age-related differences in cavity defense. Ingold (1994) also described aggressive interactions between starlings and flickers, but did not examine sex or age differences in these behaviors. Lawrence (1967) described woodpeckers defending their nests from inside their cavities, engaging in alarm vocalizations and diving attacks; she also reported a male Northern Flicker that delivered a blow with its beak to a squirrel entering a nest hole, effectively deterring the squirrel from entering.

In this study, we presented a model predator (red squirrel, *Tamiasciurus hudsonicus*) at nest sites of Northern Flickers to examine adult nest-defense behavior in relation to age, sex, brood size, body size, and body condition. Because flickers are relatively short-lived and their probability of survival is independent of age (Fisher and Wiebe 2006a), we predicted that there would be no differences in defense between young and older birds. Similarly, mark-recapture models suggest only a 2% difference in annual survival rate between the sexes (Fisher and Wiebe 2006a), and the sexes invest about equally in nestling provisioning (Moore 1995, Wiebe and Elchuk 2003). Thus, we predicted that male and female flickers would defend their broods with similar intensity. We also predicted that individuals in better condition and with larger broods would defend their nests more aggressively.

METHODS

Study site and study species.—Our study site was near Riske Creek, British Columbia (51° 52′ N, 122° 21′ W), and encompassed approximately 100 km^2; 90–120 pairs of flickers nest there each year (Fisher and Wiebe 2006a). Habitats on the site are patchy and variable. Flickers prefer grasslands for foraging (Elchuck and Wiebe 2003) and patches of quaking aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) for nesting (Martin and Eadie 1999). Continuous forests of Douglas-fir (*Pseudotsuga menziesii*) and hybrid spruce (*Picea engelmannii* × *P. glauca*) also occur.

Flickers migrate to the area in mid-April and begin egg-laying in early- to mid-May (mean clutch-initiation date = 13 May, range = 26 April–2 July; Moore 1995, KLW unpubl. data). Each year since 1998, the area has been surveyed in spring (22 April–15 May, 1998–2005) for finding newly excavated cavities and to check old cavities for new breeding pairs (flickers tend to reuse old cavities more often than other woodpeckers; Moore 1995, Aitken et al. 2002, Wiebe et al. 2006). Tape-recorded territorial playback calls also were used to locate flicker territories and nest sites. Average clutch size in this area is eight eggs and mean number of young fledged per successful nest is six (Wiebe 2003). Once a clutch was complete, we cut a small door into the side of the nest tree for access to adults, eggs, and nestlings (see Wiebe 2001). Flickers seem to tolerate the doors and readily re-use such cavities (Fisher and Wiebe 2006a). Approximately 18% of monitored nests are depredated annually by mammalian predators, mainly red squirrels (Fisher and Wiebe 2006b).

We captured flickers by flushing individuals from the nest cavity into a small net placed over the cavity entrance (Fisher and Wiebe 2006b). Three colored plastic and one aluminum band were attached to each individual to aid in individual identification (>95% of the known annual breeding population is color banded and individually identifiable). During banding, we used molt criteria to determine the birds' ages (up to 4 years old; Pyle et al. 1997). We developed an index of flicker body size (i.e., score on the first axis of a principle components analysis based on six measures: bill depth, and lengths of the wing, bill, tail, tarsus, and ninth primary) and body condition (i.e., residuals of a regression of body mass on body size); because of sexual size dimorphism, we made separate calculations for males and females (see Wiebe and Swift 2001). A year-specific estimate of body condition was made only for individuals that were trapped and weighed in 2003 and 2004; thus, only individuals captured during 2003 or 2004 were included in analyses with body condition as a covariate (see below). We assumed that body size (i.e., the structural size of an individual and not body mass) did not change from year to year.

Model presentations.—Birds with altricial young generally defend their nests most strongly during the nestling stage and as nestlings age (Montgomerie and Weatherhead 1988). We measured nest defense when nestlings were 10–15 days old to control for effects of nest stage and nestling age on defense behavior. At each nest, we tested nest defense once with a predator (taxidermic model of a red squirrel) and once with a control (taxidermic model of a Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*, or a Cedar Waxwing, *Bombycilla cedrorum*). The same individuals were tested only once with each model during the 2-year study to avoid potential habituation of parents to the models (Knight and Temple 1986a, 1986c). Blackbird and waxwing models were used as controls because they are both common in the study area and neither poses a threat to flicker broods (Wiebe 2004). In 2004, during 60% of control trials we used the waxwing because the blackbird model was irreparably damaged from transportation to and from trials.

Predator and control trials were conducted randomly at a given nest, with 1–5 days between trials (i.e., one trial = one model presentation). Because the perceived threat from a predator could vary with distance between the predator and the nest (Rätti 2000), we fastened the models at a fixed distance (1 m below the cavity entrance) with a bungee cord tied to the tree trunk. The model squirrel was attached to a small, flat board base that was then attached to the tree trunk. Control models were mounted in an upright, perched position on a natural branch, which was then attached to the tree trunk. During a given trial, territorial "chatter" calls of squirrels or songs of Yellow-headed Blackbirds or Cedar Waxwings were played at the base of the nest tree to increase model detectability (Ghalambor and Martin 2002). After models were placed at the nest, we retreated to a concealed position ≥15 m away to record responses of the returning parents.

The first variable we recorded was response time of the adult (i.e., sec between when we had set up the model and were hidden, to when the parent returned and we judged it was within 10 m of the nest and in sight of the model). Ten meters from the nest was usually the maximum distance from which we could observe a bird responding, because of dense foliage around some nests. We were confident that the flicker was responding to the model at distances ≤10 m from the nest once we judged that it could see the model. If parents did not return to within 10 m and in sight of the model in 1 hr, then these trials were removed from all analyses. After an adult(s) returned within ≤10 m, we recorded its behavior for 5 min (if both parents returned simultaneously, we treated them as individual responses). Flickers respond to models with slow, deliberate movements (Wiebe 2004), so the 5-min period should have provided a representative sample of behavior. We quantified defense levels based on four behaviors recorded during the 5-min period: (1) number of alarm calls (*peah* and *wicka* calls; Moore 1995); (2) the closest distance that the responding parent approached the model (m; a visual estimate); (3) whether or not the parent dived at or hit the model (dichotomous variable); and (4) time (sec) an individual spent inside the cavity during each trial (flickers entered cavities and then peered back out, usually with their beaks protruding from the cavity entrances). Time spent in the cavity should reflect investment in nest defense because blocking the entrance prevents predation of the nest (Cordero and Senar 1990). Assessing the risk a parent incurs by blocking the cavity entrance is difficult. This defensive strategy may be safer than others because most of the parent's body is inside the cavity (Cordero and Senar 1990); conversely, there are no avenues of escape for the parent.

Statistical analyses.—Response time was square-root transformed to meet assumptions of normality, and we analyzed it separately from other defense variables because it was unlikely to have been influenced by model type (parents presumably had not had time to see the model before returning). We used an ANCOVA to test whether age, sex, brood size, and/or body condition affected response time to the predator model (we assumed that the structural size of an individual would not influence response time). Because data transformations of the other four defense variables did not result in normality, we used non-parametric tests for subsequent analyses. Statistical significance was set at $P < 0.05$.

With respect to the four nest-defense variables, there was no difference between control model types (blackbird versus waxwing;

Mann-Whitney *U* and Fisher Exact tests: all $P > 0.47$). Similar tests also showed that there were no significant differences between years in terms of responses to control and predator models (all $P > 0.12$). Therefore, we pooled all responses (for years and control models) in subsequent analyses.

We first analyzed each defense variable singly to determine which differed significantly between control and squirrel models, without any other effects. This allowed us to eliminate model type as a variable if it was non-significant, thus simplifying subsequent models involving age class, sex, brood size, body size, and body condition. We used paired tests (Wilcoxon's signed-rank tests) to analyze minimum distance to the model, time in the cavity, and number of alarm calls to account for both predator and control trials taking place at the same nest. This approach may have been more stringent than necessary because it was not necessarily the same individual that responded to each trial; however, independent test results were consistent with those of the paired tests. We used a Fisher's exact test to compare the frequency of diving at the squirrel versus the control models. All means presented are ± SD.

After separate analysis of each defense behavior (see results), we constructed an overall defense score based on the three variables that differed significantly between control and predator models. This score was used in subsequent analyses involving the relationship between various parental attributes and strength of response to the squirrel model. A score of 1 indicated the bird returned to the nest and was judged to be within sight of the model but did not dive at the model or enter the cavity, and always remained ≥2 m away from the model (there is a low probability that a squirrel could contact the parent at a distance of 2 m). A score of 2 indicates that the parent approached ≤1 m from the predator model but otherwise performed no other nest-defense behaviors. In developing score 2, we assumed that a squirrel might be able to physically contact a flicker ≤1 m away and that parents approaching within 1 m were placing themselves at a greater risk than those in score category 1. Responses in category 2 included perching on the cavity lip from the outside or on a branch within 1 m of the model. A score of 3 indicates that the parent entered the cavity and blocked it from the inside. Finally, a score of 4 indicates that birds dived at or hit the model, indicating the riskiest and most energetically expensive behavior to a defending adult.

TABLE 1. Sample sizes of Northern Flickers responding to a model predator (red squirrel) or control (Yellow-headed Blackbird or Cedar Waxwing) placed at their nests during the brood-rearing stage at Riske Creek, British Columbia (2003 and 2004 data pooled). Totals include instances in which both parents responded to the models, plus those in which only one parent responded; thus, sample sizes are larger than the total number of trials conducted for each model type.

Model type (total no. trials)	Sex	Age	*n*
Control (91)	Male	1 year	15
		2 years	17
		3+ years	25
	Female	1 year	19
		2 years	16
		3+ years	15
Predator (94)	Male	1 year	17
		2 years	19
		3+ years	24
	Female	1 year	20
		2 years	14
		3+ years	13

For statistical analyses involving age, we categorized males or females as either 1, 2, or 3+ years old, such that there was at least a sample size of 13 in each age category (Table 1). A further subdivision of age was not possible to analyze statistically, as it would have resulted in some categories with a sample size <5. We used a Kruskal-Wallis test to examine whether the median defense scores of birds in the six different age-sex classes differed. To analyze the effect of brood size on defense score (a categorical variable), we used Spearman's rank correlations. Body size and condition met assumptions of normality; therefore, we could use parametric tests (two-factor ANOVA) to assess the relationship between defense score and sex on body size and condition (dependent variables).

RESULTS

We conducted 91 control trials and 94 predator trials at 94 Northern Flicker nests in 2003 and 2004. Control trials were not conducted at three nests because nestlings were >15 days old by the time the second model could

TABLE 2. Effects of sex, age class (1, 2, and 3+ years old), brood size, and body condition of flicker parents on their response time (see description in text) to a model nest predator presented at the nest during the brood-rearing stage at Riske Creek, British Columbia, 2003 and 2004. No predictor was significant according to a 2-factor ANCOVA (n = 84 individuals) using Type III sums of squares.

Effect	SS	df	*F*	*P*
Sex	231.67	1	1.18	0.29
Age	181.15	2	0.44	0.65
Sex × age	438.81	2	1.06	0.35
Brood size	16.50	1	0.56	0.46
Body condition	589.02	1	2.84	0.10
Sex × brood size	211.50	1	1.02	0.32
Age × brood size	92.43	2	0.22	0.80

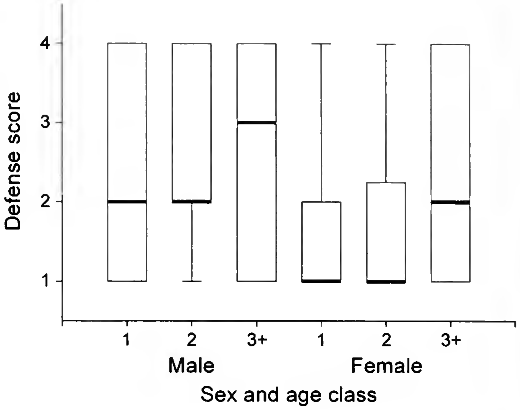

FIG. 1. Nest-defense scores of parent flickers did not differ by sex and age categories when responding to a model predator (red squirrel) placed at their nest during the brood-rearing stage in Riske Creek, British Columbia, 2003 and 2004. Bold horizontal lines represent median defense scores, boxes represent 25th and 75th percentiles, and error bars represent 10th and 90th percentiles. Because several birds within each age and sex category received the same defense score, some 10th, 25th, 75th, and 90th percentiles overlap; thus, symbols for each age and sex class are not necessarily apparent.

be presented. Parents occasionally returned together to defend the nest (16 out of 91 control and 13 out of 94 predator trials) and responses by these individuals were considered to be independent trials (i.e., two parents responding increased sample size by two). Sample sizes of responding parents of both age classes and sexes varied according to model type (Table 1).

Response time and defense behaviors.—The mean overall response time to the predator model was 1,090 ± 876 sec (n = 107). There was a weak trend (P = 0.10) that birds in better condition responded to the predator model more quickly, but there was no effect of age, sex, brood size, or body condition, and there were no interactions (Table 2).

Flickers dived significantly more at the predator model (26% of trials) than at the control (2% of trials; Fisher's exact test: $P <$ 0.001). Parents also approached the predator model more closely (3 m ± 4) than the control model (5 m ± 4; Wilcoxon's signed-rank test: $Z = -4.98$, $P < 0.001$). During the 5-min trials, flickers spent significantly more time in their cavities when responding to the predator model than to the control model (16% ± 33 versus 5% ± 20, respectively; Wilcoxon's signed-rank test: $Z = -2.35$, $P < 0.001$). Parents gave *wicka* and *peah* alarm calls in 36% of the trials, but there was no effect of model type on the number of alarm calls (mean number of alarm calls = 11 ± 32 and 18 ± 37 in response to predator and control models, respectively; Wilcoxon's signed-rank test: Z = -1.41, P = 0.16).

Traits of the parent and brood.—The median defense score for males ≥3 years of age was marginally higher that than of any other age-sex category (Kruskal-Wallis test: χ^2 = 6.63, df = 3, P = 0.085; Fig. 1). Brood sizes of parents tested with the squirrel model ranged from 2 to 9, but there were no significant correlations between brood size and nest-defense score for the six age-sex classes when considered separately (Spearman's rank correlations: all $P > 0.28$, but two-year old males showed a marginally significant trend of defending smaller broods more aggressively, $r = -0.45$, P =0.060). Similarly, with all ages and sexes combined, there was no effect of brood size on defense score (Spearman's rank correlation: r = 0.02, P = 0.83). In another analysis, we categorized brood sizes as small (≤6 chicks, n = 45) versus large (≥7 chicks, n = 62). Approximately 30% of individuals with large broods exhibited the most intense defensive behavior (score = 4), whereas 22% of individuals with small broods had score 4; however, the overall frequency of

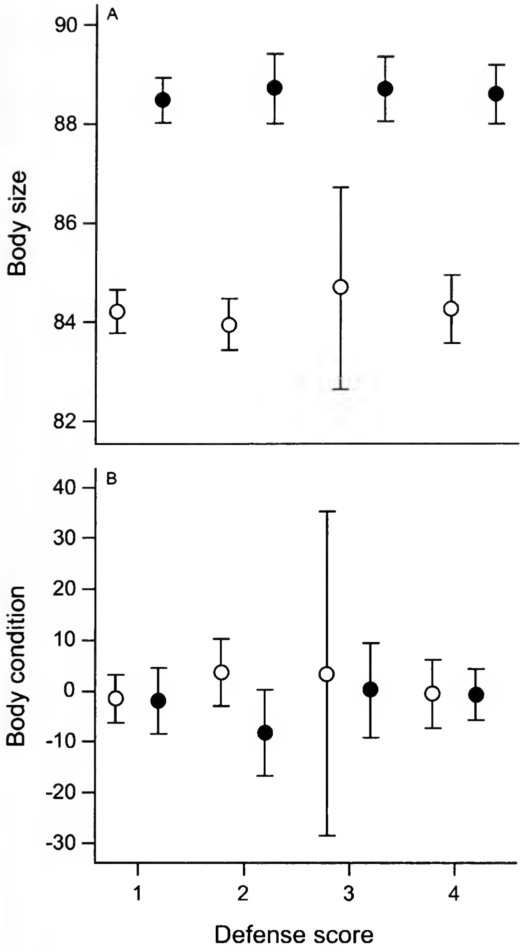

FIG. 2. Mean and 95% CI of (A) body size and (B) body condition for male (filled circles) and female (open circles) Northern Flickers performing four levels of nest defense (1= least, 4 = greatest; see text for description of defense scores) in response to a model predator placed at nests during the brood-rearing stage at Riske Creek, British Columbia, 2003 and 2004. Body size differed between the sexes, but defense scores did not vary with body size or condition.

defense scores was not associated with brood size (χ^2 = 2.48, df = 3, P = 0.48).

As expected, adult body size was significantly associated with sex (males were structurally larger than females; two-factor ANOVA: F = 345.67, df = 1, $P < 0.001$), but there was no relationship between body size and defense score (F = 0.33, df = 3, P = 0.80; Fig. 2), nor was there a sex × defense score interaction (F = 0.41, df = 3, P = 0.75). Similarly, there was no relationship between body condition and defense score (two-factor ANOVA: F = 1.48, df =3, P = 0.84) for either sex (F = 2.13, df = 1, P = 0.15; Fig. 2) or a sex × defense score interaction (F = 1.48, df =3, P = 0.23; Fig. 2).

DISCUSSION

Relationship between sex and nest defense.—Although a model predator may not elicit the same intensity of nest defense as a real predator, the fact that flickers responded to it more intensely than to the control model suggests that they did perceive danger. Consistent with initial predictions, we found no differences between nest defense of male and female flickers. Although many studies have revealed sex-related differences in nest defense among birds (Gill and Sealy 1996, Cawthorn et al. 1998, Pavel and Bureš 2001, Griggio et al. 2003), others have not, including studies on the American Goldfinch (*Carduelis tristis*; Knight and Temple 1986b) and Red-backed Shrike (*Lanius collurio*; Tryjanowski and Golawski 2004). Adult male and female American Goldfinches may exhibit equal defense responses because they are monogamous and both sexes are required to raise the young (Knight and Temple 1986b). Tryjanowski and Golawski (2004) suggested that net costs and benefits of nest defense by male and female Red-backed Shrikes were equal because males were larger than females, but females had greater confidence of parenthood. For flickers, the sex-related differences in survival (male survival is 2% lower than that of females; Fisher and Wiebe 2006b), body size (males are ~3% larger than females; Moore 1995, Wiebe 2000), and investment in the current brood (Moore 1995, Wiebe and Elchuk 2003) are likely too small to alter the costs and benefits of sex-related nest defense. Among cavity nesters, male Eastern Screech-owls (*Otus* [currently *Megascops*] *asio*) defend nestlings more aggressively than females (Sproat and Ritchison 1993), as do male Great Tits (*Parus major*; Currio and Onnebrink 1995) and male Tree Swallows (*Tachycineta bicolor*; Winkler 1992).

Age and nest defense.—In general, we found no significant association between age and nest defense, although males ≥3 years old tended to engage in more risky defense behavior (attributed to their greater tendency to block the cavity entrance) than the other groups. Blocking the cavity entrance may be used by cavity nesters to prevent usurpation of cavities (Cordero and Senar 1990). With the head and bill in striking position at the entrance hole, it also may be an effective strategy for fending off an attack while minimizing risk to the rest of the parent's body. The lack of strong age or sex effects on any defense behavior suggests that individuals of different ages perceive the overall costs and benefits of nest defense in a similar way.

According to economic models of nest defense (Montgomerie and Weatherhead 1988), an older bird should defend its current brood more aggressively than a younger bird because it has a lower future reproductive potential; however, we found no evidence for this in flickers. Winkler (1992) explained that age-independent survival probabilities precluded an effect of age on nest defense by Tree Swallows. Similarly, the annual apparent survival rates (42%) for flickers do not vary with age, and the birds are relatively short-lived (Fisher and Wiebe 2006b), so it is probably not surprising that age has little influence on defense intensity.

Although future reproductive potential is one component that could lead to age-dependent nest defense, experience also may be a key factor if defense is learned and becomes less risky for the adult over time (Montgomerie and Weatherhead 1988). We could not separate age from experience in our study and it is impossible to know the previous experience that a wild bird may have had with a predator.

Effects of body size and condition on nest defense.—It was surprising that neither body size nor condition were positively associated with our measures of flicker nest defense. Although sexual-size dimorphism is often cited as contributing to differences in nest defense between the sexes (Tryjanowski and Golawski 2004), effects of body-size differences within the sexes have rarely been tested (Hamer and Furness 1993, Radford and Blakey 2000). If large and small birds are both effective nest defenders for different reasons—for example, if small individuals have greater maneuverability and large individuals are more powerful—then overall costs and benefits may be similar for each (Montgomerie and Weatherhead 1988). The few studies that have tested for within-sex effects of body condition have been equivocal at best, ranging from no effect (Radford and Blakey 2000) to a sex-specific effect (Winkler 1992, Hamer and Furness 1993). There is little direct evidence that body condition affects the intensity of active defense in any species, but good nutrient reserves may allow a parent to reduce foraging time away from the nest and be more attentive to the nest site during incubation and brooding (Slagsvold and Lifjeld 1989, Wiebe and Martin 1997); in turn, these factors would result in greater nesting success (Chastel et al. 1995). We found some evidence that birds in better body condition responded more quickly to the predator model, which may provide support for this hypothesis. Flicker condition was measured in the late stages of incubation or early stages of brooding when parents could be captured; thus, they may not have been in exactly the same condition at the time of our defense trials (about 10–15 days later). However, if relative rankings of body condition among individuals remain similar, we should have been able to detect a pattern.

Effects of brood size on nest defense.—We predicted that male and female flickers with larger broods should defend them more aggressively than flickers with smaller broods, but brood size was not correlated with any of the defense behaviors that we measured. Tryjanowski and Golawski (2004) suggested that brood size manipulation experiments are needed to adequately test for effects of brood size on nest defense. However, even some experimental studies have failed to reveal any differences in nest defense as a result of brood size (Tolonen and Korpimäki 1995). If parents optimize their clutch size according to their ability to raise all their young, then large and small broods may represent equal value to the defending adults, in which case brood size may not be expected to influence nest defense (Tolonen and Korpimäki 1995, Dawson and Bortolotti 2003).

In summary, anecdotal data from the literature (Lawrence 1967) and video-tape evidence from our own study site (KLW unpubl. data) indicates that the defense behaviors we observed may successfully protect cavity nests from live predators, such as red squirrels. Individual flickers varied in their responses, but we were unable to find strong correlates of that variation associated with common traits of those individuals or their broods.

ACKNOWLEDGMENTS

We sincerely thank C. L. Galatiuk, H. J. Kalyn, J. P. M. Johnston, and K. M. Warner, who helped with the model presentations. We would also like to thank K. Martin, who allowed us to conduct model presentations on parts of her study area. D. J. Ingold, J. J. Kappes, Jr., and one anonymous reviewer improved earlier drafts of this manuscript. This project was funded through National Sciences and Engineering Research Council of Canada and Southern Interior Bluebird Trail Society scholarships to RJF, and through a National Sciences and Engineering Research Council of Canada operating grant to KLW. We would also like to thank the Borror Acoustics Laboratory for providing squirrel and blackbird vocalizations used in the model presentations.

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The Wilson Journal of Ornithology 118(4):461–470, 2006

BLACK-THROATED BLUE WARBLER AND VEERY ABUNDANCE IN RELATION TO UNDERSTORY COMPOSITION IN NORTHERN MICHIGAN FORESTS

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ABSTRACT.—Balsam fir (*Abies balsamea*) understory may be an important predictor of Black-throated Blue Warbler (*Dendroica caerulescens*) and Veery (*Catharus fuscescens*) distributions in northern hardwood forests that are heavily browsed by white-tailed deer (*Odocoileus virginianus*). We examined the abundance and age ratios of Black-throated Blue Warblers, and the abundance of Veerys, in 16 plots of hardwood forest with different understory composition within a heavily browsed region of the Hiawatha National Forest in Michigan's eastern Upper Peninsula. Four of these 36-ha plots had minimal understory and 12 had dense understory with variable amounts of balsam fir. Black-throated Blue Warbler abundance was significantly greater in plots with an average of 27% balsam fir understory cover than in plots dominated by deciduous understory; no Black-throated Blue Warblers were detected on the minimal understory plots. Age ratios did not differ significantly relative to balsam fir understory density. Veery abundance also did not vary with balsam fir understory density, but it increased with overall understory density. In forests such as these, where deer are abundant but rarely browse balsam fir, active management of balsam fir understory could provide key habitat for sustaining populations of Black-throated Blue Warblers and Veerys. We recommend that managers consider the presence of balsam firs in the understory when planning forest harvests in deer-impacted areas, so that they leave some balsam fir and stagger the cutting of stands with balsam fir over time to create and maintain heterogeneous understory structure. *Received 2 September 2005, accepted 16 May 2006.*

Identifying key habitat characteristics that predict songbird distributions represents an important step towards incorporating songbirds into forest management plans (Martin 1992, Donovan et al. 2002). In the eastern United States, browsing of understory vegetation by white-tailed deer (*Odocoileus virginianus*) produces forests that differ in terms of their structural characteristics and plant species compositions from those in less impacted areas (reviewed by Rooney and Waller 2003, Côté et al. 2004), and these changes can affect the abundance of understory-dependent songbirds (Casey and Hein 1983, deCalesta 1994, McShea and Rappole 2000). Browsing impacts, however, are likely to differ across species' ranges because of variation in the plant community, the landscape context, and, in the Great Lakes region, the degree to which the understory is protected from deer by snow. Therefore, predicting the abundance of understory-dependent birds is best approached using habitat indicators based on local information, a key element of which may be the distribution of browse-resistant plants.

We investigated the relationship between understory characteristics and the abundance of two forest songbird species, the Black-throated Blue Warbler (*Dendroica caerulescens*; BTBW) and the Veery (*Catharus fuscescens*), in managed northern hardwood forests in the eastern Upper Peninsula of Michigan, where the overabundance of deer is a conservation concern (The Nature Conservancy 2000, Rooney and Waller 2003, Kraft et al. 2004). Our sites were dominated by sugar maple (*Acer saccharum*) and located near coniferous forest "deeryards"—areas that provide winter habitat for high densities of deer (Van Deelen et al. 1998). At similar Great Lakes forest sites, browsing has decreased understory density and reduced structural complexity, especially for sugar maple seedlings and saplings (Alverson et al. 1988, Kraft et al. 2004).

Veerys and BTBWs are likely to be susceptible to browsing impacts because they nest and forage in the understory (Holmes 1994, Moskoff 1995). Both species are also of con-

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servation concern in northern forests (U.S. Fish and Wildlife Service 2002; Matteson et al. in press). BTBWs have been studied intensively in New Hampshire, where population density is positively associated with shrub and sapling density (Steele 1992, 1993; Holmes et al. 1996), and the density of deciduous leaves in the shrub layer is a key predictor of territory quality (Rodenhouse et al. 2003). Less is known about key habitat features for Veerys but, in Michigan, they are typically found in mesic to wet forest with dense understory and a conifer component (Winnett-Murray 1991).

We hypothesized that the density of understory balsam fir (*Abies balsamea*), a species rarely browsed by deer in our region (Borgmann et al. 1999), may better predict BTBW abundance than deciduous species in Great Lakes forests. Our previous work in Michigan hardwood forests near deeryards revealed that 100-m-radius point-count locations with abundant balsam fir had higher relative abundances of BTBWs than locations with dense, deciduous-dominated understory (Hall 2002). In this paper, we considered a management-relevant scale (36-ha stand) and compared BTBW and Veery abundance between plots that varied in their proportion of balsam fir understory. We also predicted that areas with more balsam fir would have a higher ratio of older to yearling BTBWs, thus indicating habitat preference (Holmes et al. 1996, Hunt 1996).

METHODS

Study area.—We collected data in 16 stands of mature, relatively even-aged hardwood forest within a section (~15 × 7 km^2) of the southeastern Hiawatha National Forest in Mackinac County, Michigan, between 46° 09′ 06″ N to 46° 05′ 18″ N and 84° 52′ 23″ W to 84° 40′ 50″ W (Fig. 1). All plots were located within the St. Ignace subsection of the Niagaran Escarpment, an area characterized by shallow morainal soils and occasional glacial erratics (Albert 1995). Sugar maple was the dominant overstory tree on the study plots, but often was co-dominant with American beech (*Fagus grandifolia*) and, to a lesser extent, aspen (*Populus* spp.), paper birch (*Betula papyrifera*), and American basswood (*Tilia americana*); rarely, balsam fir and white pine (*Pinus strobus*) were also co-dominant. Typical understory species included sugar maple, hop-hornbeam (*Ostrya virginiana*), and balsam fir; occasionally we found seedlings and saplings of other canopy species and white spruce (*Picea glauca*), white ash (*Fraxinus americana*), and black cherry (*Prunus serotina*). The study area receives an annual average of 1.5–2 m of snow (Albert 1995), which appears to protect many plants from being completely removed by overwintering deer that seek shelter in the nearby deeryards and enter these stands to forage.

We chose site locations using a 2002 GIS database of forest management units in the Hiawatha National Forest within the Niagaran Escarpment (U.S. Department of Agriculture Forest Service unpubl. data). We used ArcView (Environmental Systems Research Institute 2002) to select hardwood management units large enough to accommodate a square 36-ha plot, then visited those units in random order for the purpose of selecting our 16 sites, with four in each of the following understory categories: (1) minimal understory vegetation, (2) deciduous-dominated understory vegetation with sparse balsam fir, (3) understory vegetation with moderate balsam fir density, and (4) understory vegetation with high balsam fir density (Fig. 1). The initial assignment of sites to understory categories was based on visual estimates conducted in May, prior to the standardized collection of vegetation data (see below). The dark vegetated areas (Fig. 1) were dominated by coniferous overstory and comprised the habitat type typical of deeryards in this region (Van Deelen et al. 1998). The 36-ha plot size was small enough so that sites were internally similar (e.g., within the same management unit, with similar canopy cover and understory density, and with few old logging roads or other openings), yet large enough to encompass a wide range in the number of BTBW territories (typically 1–4 ha in size; Holmes 1994, Hall 2002).

Vegetation sampling.—We measured understory composition using a modified method from Mueller-Dombois and Ellenberg (1974). Within each plot, we established three parallel, 600-m transects spaced 200 m apart, and randomly oriented the transects east-west or north-south. We then divided each transect into 100-m segments and randomly chose a 16-m^2 quadrat within each segment, for a total

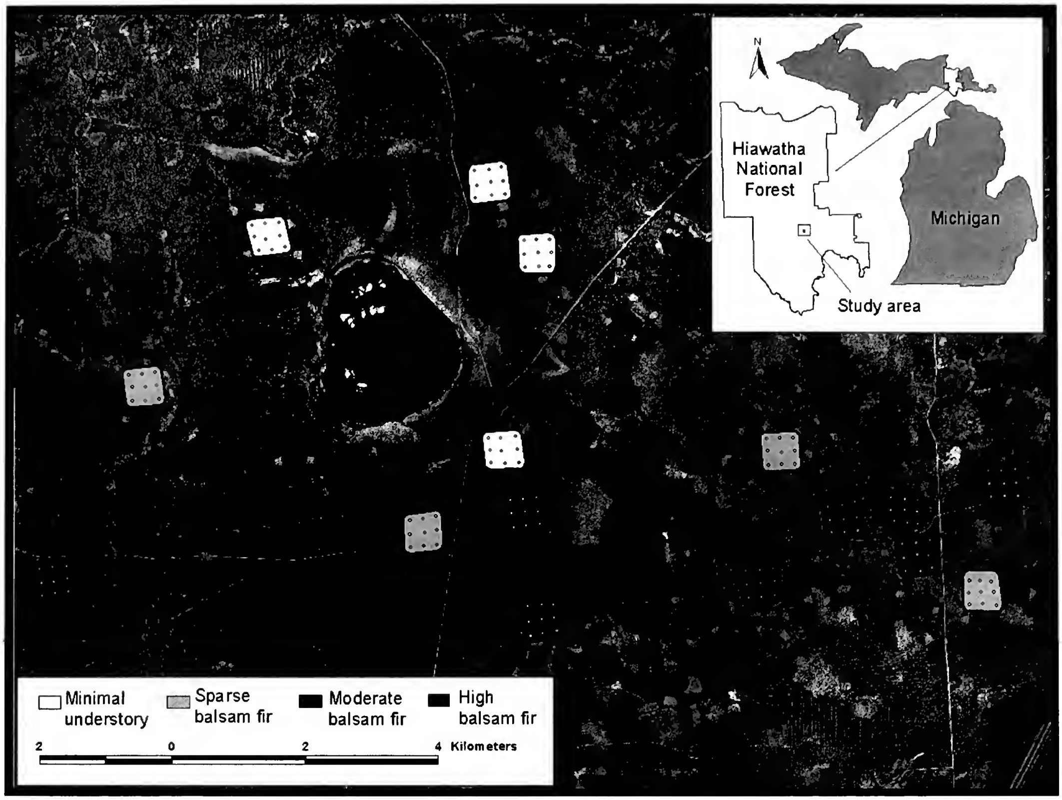

FIG. 1. Distribution of four understory vegetation plot types in the Hiawatha National Forest, Mackinac County, Michigan, summers 2002 and 2003. Digital orthophoto taken before leaf-out in March 2001 shows conifer stands in dark gray, hardwood stands in light gray, and water in near black. Squares represent 36-ha plots (n = 16): white = minimal understory, light gray = deciduous-dominated understory with sparse stem densities of balsam fir, dark gray = understory with moderate balsam fir density, black = understory with high balsam fir density. Points in each plot (n = 9) represent approximate locations of 100-m radius avian point counts and 11.3-m overstory sampling subplots. (Sources: Environmental Systems Research Institute 2002 Projection: UTM Zone 16 N, Datum: NAD 1927; U.S. Department of Agriculture Forest Service unpubl. data.)

of 18 quadrats per plot. For each quadrat, we calculated the total stem count and average percent cover of woody understory plant species within six height categories—five 0.5-m categories (ranging from 0.5 to 3 m) and a 3- to 5-m category—based on estimates from four 4-m^2 sub-quadrats. Using a spherical densiometer, we also measured the canopy cover in each quadrat. Following a modification of James and Shugart's (1970) vegetation sampling method, in each 36-ha plot we established nine points spaced 200 m apart on a 3 × 3 grid (Fig. 1); within an 11.3-m radius of each point, we counted the number of trees in two size categories (small: 7.5–22.5 cm in diameter at breast height [dbh], large: ≥22.5 cm dbh). We sampled all vegetation between late July and September, prior to leaf fall, in 2002 and 2003.

We calculated mean stem density, percent cover, and height for both balsam fir and deciduous understory species from the 18 quadrats in each plot. We calculated the standard deviation of percent cover as a measure of understory patchiness. We used the standard deviation of height as a measure of understory vertical structure. We also determined mean density of small and large trees in the 11.3-m point samples.

Bird sampling.—In 2002, we measured the abundance of territorial male BTBWs by target-netting and color-banding birds. An observer (LJK) first surveyed each plot during late May–early June by walking the three transects and using song playbacks to detect and record the locations of BTBWs; Wolf et al. (1995) estimated that BTBW song is detectable up to 120 m from an observer. Plots were revisited up to 10 more times between late May and late July, depending on the density of male BTBWs and how catchable they were. During these visits, two or three observers once again searched the plots for male BTBWs by walking transects and using song playbacks; nearly all males within each plot were captured and color-banded by targeted mist-netting (song playback and model bird). We banded each bird with a federal aluminum leg band and two colored plastic leg bands. During banding, we determined age as older (after second year; ASY) or yearling (second year; SY) on the basis of plumage characteristics (Pyle 1997). Experienced observers (KRH, LJK) aged three uncatchable birds by using binoculars to study their plumage characteristics (Graves 1997a). Between late May and early June 2003, we systematically resurveyed all plots using song playback to determine 2003 abundance.

From early June to mid-July 2002, we conducted 10-min point counts (100-m fixed radius) of singing males to estimate the relative abundances of Veerys and BTBWs (as a second measure) in each plot (Ralph et al. 1993). For each bird, we recorded its location within one of three distance categories (0–25, 25–50, 50–100 m) and time to detection (0–3, 3–5, 5–10 min). Weather permitting, LJK surveyed one plot per day, starting the count within 30 min of sunrise. After randomly selecting a starting point from one of the nine points within a given plot (Fig. 1), the observer conducted the count following the most efficient route. We minimized the potential for double-counting birds that moved between survey points by eliminating individual detections in similar locations on adjacent counts. Since BTBWs often move quickly across large territories (e.g., >200 m in diameter; Hall 2002), double-counting birds during point counts was a particular concern. Thus, our BTBW analyses focused on the banding data, whereas we used the point count data only as an additional measure of BTBW abundance and to verify that we had banded all birds in locations where they were detected during point counts.

TABLE 1. Eigenvectors of the first three principal components for 13 vegetation variables measured in 36-ha plots (n = 16) in the Hiawatha National Forest, Michigan, summer 2002. The standard deviation (SD) of percent cover for the 18 16-m^2 quadrats in each plot was a measure of vegetation patchiness; the SD of average height was a measure of vertical structure.

	Eigenvectors		
Variable	PCA1	PCA2	PCA3
Canopy cover	−0.14	−0.32	−0.07
Large-tree density	−0.30	−0.33	0.20
Small-tree density	0.36	0.06	−0.02
Balsam fir			
Stem density	0.37	0.03	−0.04
Percent cover	0.38	0.03	0.01
Cover SD	0.37	0.06	−0.14
Height	0.31	0.09	−0.00
Height SD	0.36	0.11	−0.01
Deciduous spp.			
Stem density	−0.19	0.44	−0.10
Percent cover	−0.21	0.51	−0.10
Cover SD	−0.21	0.47	0.04
Height	0.02	0.24	0.61
Height SD	0.04	0.16	0.65

Statistical analyses.—We performed Principle Components Analysis (PCA) using the correlation matrix for 13 vegetation variables to explore the relationship between vegetation characteristics in the 16 plots and to evaluate our visual estimates of plot characteristics. We investigated the relationships of BTBW abundance and age ratio (percent older birds), and Veery abundance, to plot characteristics by comparing the bird variables among plot types (Kruskal-Wallis test, $\alpha = 0.05$; Zar 1999) and by correlating abundance with plot scores for principal components with eigenvalues >1. Statistical analyses were conducted in S-Plus 6.1 (Insightful Corporation 2002). Means are presented ± SE.

RESULTS

Vegetation.—Principle components analysis identified three axes that accounted for 84% of the variation in vegetation measurements. The first principle component, which accounted for 50% of the variation (eigenvalue = 6.5), positively weighted all balsam fir variables and small-tree density, and negatively weighted deciduous understory and large-tree density (Table 1). This component distinguished the eight plots classified by visual es-

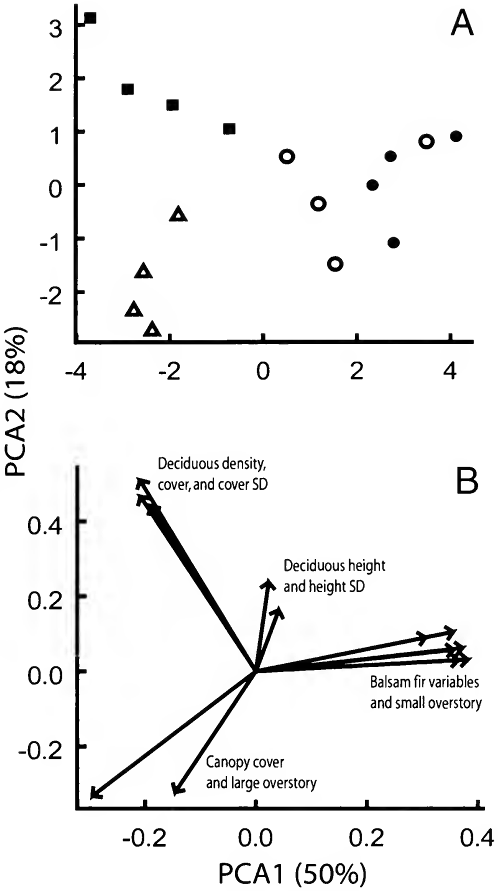

FIG. 2. Principal components analysis (PCA) showing variation in vegetation composition and structure among 36-ha plots (n = 16) in the Hiawatha National Forest, Michigan, summer 2002. (A) Plot-type distribution: triangles = minimal understory plots, squares = deciduous-dominated understory with sparse stem densities of balsam fir, open circles = understory with moderate densities of balsam fir, and closed circles = understory with high densities of balsam fir. (B) Pattern of variables along PCA axes. Axes 1 and 2 accounted for 50% and 18%, respectively, of the variation among plots. The first component positively loads balsam fir variables and the second positively loads stem density, percent cover, and patchiness of deciduous vegetation, thus separating plots containing minimal understory from deciduous-dominated understory; plots containing moderate and high stem densities of balsam fir were not clearly separated.

timation as containing moderate to high densities of balsam fir in the understory from the four minimal understory and four deciduous-dominated understory plots (Fig. 2A). Stem density of balsam fir in the understory and small-tree overstory were highly correlated (Fig. 2B). The second principle component, accounting for 18% of the variation (eigenvalue = 2.3), positively weighted deciduous understory stem density, cover, and patchiness and negatively weighted large-tree density (Table 1, Fig. 2B). This component distinguished the four minimal understory plots from the four deciduous, sparse balsam fir understory plots. The third principle component described 16% of the variation (eigenvalue = 2.0) and positively weighted deciduous understory height and vertical structure (Table 1); this component was not clearly associated with the four understory plot types.

Based on the results of the PCA, we redefined the understory categories of plots, reducing the number to three categories: minimal understory (n = 4), deciduous-dominated understory (n = 4), and balsam fir-dominated understory (n = 8). Compared to balsam fir-

TABLE 2. Mean vegetation and avian measurements (SE) for plot types after redefinition by principle components analysis: minimal understory ($n = 4$), deciduous-dominated understory ($n = 4$), and balsam fir-dominated understory ($n = 8$) in the Hiawatha National Forest, Michigan, summers of 2002 and 2003. Vegetation variables included measures with the largest loadings for the first three principle components and densities of overstory trees; plot types were subsequently defined by the PCA results. Deciduous- and balsam fir-dominated plots had similar total understory cover but differed with respect to composition; minimal understory plots contained more large (≥22.5 cm in diameter at breast height) trees. There were significant differences in the abundances of Black-throated Blue Warblers (BTBW) and Veerys by plot type (Kruskal-Wallis test, $P < 0.05$); between-plot differences in the ratio of older to younger male BTBWs were not significant (Kruskal-Wallis test, $P = 0.49$).

	Plot type		
Variable	Minimal understory	Deciduous-dominated understory	Balsam fir-dominated understory
Large-tree density (stems/ha)	240 (9)	162 (10)	128 (7)
Small-tree density (stems/ha)	283 (25)	306 (14)	487 (24)
Balsam fir understory			
Cover (%)	0.0 (0)	2.5 (2.5)	26.9 (2.5)
Height (m)	0.50 (0.50)	0.60 (0.35)	1.51 (0.07)
Height SD	0.09 (0.09)	0.28 (0.19)	0.83 (0.14)
Deciduous species understory			
Cover (%)	12.0 (1.9)	36.0 (5.7)	12.6 (2.1)
Height (m)	1.27 (0.14)	1.33 (0.15)	1.25 (0.10)
Height SD	0.91 (0.17)	0.98 (0.09)	0.94 (0.16)
Black-throated Blue Warbler			
Abundance (2002 banding)	0.0 (0)	3.5 (0.6)	7.1 (1.0)
Abundance (2002 point counts)	0.0 (0)	3.8 (0.9)	5.2 (0.5)
Abundance (2003 survey)	0.0 (0)	3.3 (1.0)	6.4 (1.0)
Age ratio (% older)	NA	58.8 (21.2)	77.8 (7.2)
Veery			
Abundance (2002 point counts)	1.3 (0.5)	6.5 (1.3)	4.2 (0.9)

and deciduous-dominated understories, minimal understory plots were characterized by sparse understory cover, all of which was deciduous (Table 2). Plots containing deciduous-dominated understory had a moderate amount of understory cover but sparse balsam fir understory cover (2.5% ± 2.5), whereas balsam fir-dominated plots contained moderate understory cover, of which 26.9% ± 2.5 was balsam fir (Table 2). Deciduous stems typically fell in the shortest height category: in the 12 plots with the densest understory (deciduous- and balsam fir-dominated), 66% ± 4 of the stems were 0.5–1 m tall, whereas only 15% ± 2 and 19% ± 3 fell in the 1–2 m and >2 m categories, respectively. In contrast, 40% ± 3 of the balsam firs were 0.5–1 m tall; a similar percentage were 1–2 m tall (41% ± 3), and a lower percentage (18% ± 3) fell in the >2-m height category. Finally, there were fewer large trees in the twelve plots with dense understory, and more small trees in the balsam fir-dominated plots (Table 2).

Birds.—Sixty-seven BTBWs were banded in 12 plots and 3 additional males were repeatedly observed and counted, resulting in 2–12 males per 36-ha plot. The three measures of BTBW abundance (2002 banding and point counts, and 2003 repeat surveys) were highly correlated ($r = 0.90$–0.92, $n = 16$) and the results of our analyses using each of these measures were identical. BTBW abundance differed between plot types (Kruskal-Wallis test: $k = 3$; $n_{\text{minimal}} = 4$, $n_{\text{deciduous}} = 4$, $n_{\text{fir}} = 8$; $P < 0.01$ for all three abundance measures). On average, there were 1.4 to 3.6 more BTBWs per 36 ha (low estimate: 2002 point counts; high estimate: 2002 banding data) on plots averaging 27% balsam fir understory cover than on plots with sparse balsam fir (Table 2). The positive relationship between balsam fir and BTBW abundance was apparent

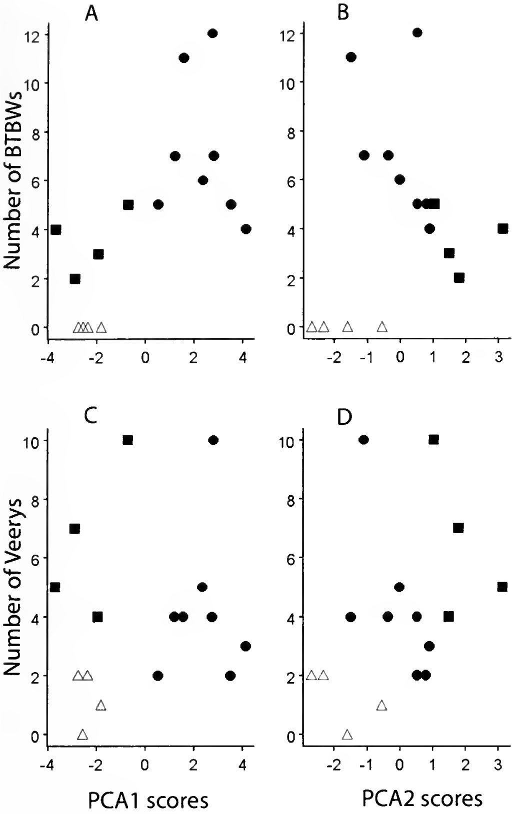

FIG. 3. Relationships between Black-throated Blue Warbler (BTBW) and Veery abundances and the scores for vegetation characteristics summarized by principal components analysis (PCA) for 36-ha plots (n = 16) in the Hiawatha National Forest, Michigan. BTBW abundance (based on banding data) in 2002 versus scores for (A) PCA 1 and (B) PCA 2; Veery relative abundance (based on point counts) in 2002 versus scores for (C) PCA 1 and (D) PCA 2. Triangles = minimal understory plots, squares = deciduous-dominated plots, and circles = balsam fir-dominated plots. For the plots that contained dense understory (n = 12), BTBW abundance increased significantly with increasing values of PCA 1 (r = 0.68), and decreased significantly with increasing PCA 2 (r = −0.65). Veery abundance was not linearly related to the PCA scores.

when BTBW abundance was compared to the first principal component (r = 0.68, n = 16, P = 0.004; Fig. 3A). Excluding plots with minimal understory, BTBW abundance showed a negative association with deciduous understory (r = −0.65, n = 12, P = 0.021; Fig. 3B). There was no relationship between BTBW abundance and the height of deciduous understory, as measured by the third principle component (r = −0.25, n = 16, P = 0.35).

Overall, 74% (52 of 70) of the BTBWs were older males in 2002. The BTBW age ratio (% older) did not differ significantly between plot types (Kruskal-Wallis test: k = 2, χ^2 = 0.47, P = 0.49; Table 2) and showed no pattern of relationship with any of the principal components (n = 12, P > 0.25 for all three correlations).

Veery relative abundance differed significantly by plot type (Kruskal-Wallis test: k = 3, χ^2 = 9.12, P = 0.010) and there were no significant differences among the plot types in detection probabilities by distance or time (distance: χ^2 = 3.41, P = 0.065; time: χ^2 = 2.14, P = 0.14; n = 65). Veery abundance was somewhat greater in plots with abundant deciduous understory than it was in balsam fir-dominated plots and there were few Veerys in minimal understory plots (Table 2). Veery abundance did not show any relationship to the three principle components (n = 16, P > 0.20 for all three correlations; Fig. 3C, D). Thus, Veery abundance increased with understory cover, but did not show a pattern with respect to understory type (Table 2).

DISCUSSION

In maple-dominated, managed stands in the Hiawatha National Forest that experience high winter deer densities, Black-throated Blue Warbler abundance was significantly greater in areas with a dense understory of balsam fir than in areas with a dense understory of deciduous trees. Previous studies have shown that BTBWs breed in both pure stands of northern hardwoods and mixed stands of hardwood-conifer, and exhibit little preference for particular understory species if dense cover exists (Steele 1993, Holmes 1994, DeGraaf et al. 1998, Steffes 1999). In New Hampshire, BTBWs often nest in hobblebush (*Viburnum alnifolium*), a shade-tolerant deciduous shrub, probably because it is abundant and provides structural characteristics and branch heights suitable for nesting (Holway 1991, Holmes 1994). Hobblebush and shrubs with similar characteristics (e.g., *Rhododendron* spp.) used by nesting BTBW in other parts of the species' range (Holmes 1994) do not occur in most Great Lakes forests, and we suggest that at sites like ours, where most of the understory comprises regenerating tree species, balsam fir can play a role similar to that of hobblebush, particularly in areas where deer browsing reduces the abundance and heights of deciduous species. Therefore, the proportion of balsam fir in the understory, which ranged in our study from 0–40% cover in plots with 3–53% total understory cover, can be a useful tool for predicting the occurrence of BTBWs in managed, maple-dominated stands.

BTBW densities in our study area, which is near the western edge of the species' range, were low compared to those in more central parts of their range (e.g., New Hampshire, the Appalachians); this result agrees with estimates from Breeding Bird Survey data (Holmes 1994) and work by Graves (1997b). Densities averaged 0.16 ± 0.02 males/ha in plots where BTBWs were present (n = 12, maximum = 0.3), versus 0.8–0.9 males/ha in New Hampshire forest with a dense shrub layer (Holmes 1994). The presence of balsam fir and some short (<1 m) deciduous understory (presumably present due to snow protection) appears to allow BTBWs, Veerys, and other understory-dependent species to persist in these heavily deer-impacted hardwood forests. For both bird species, the peak relative abundance values were similar to high values observed in Michigan forests with much less evidence of browsing by deer (Hall 2002). Our results indicate that if local forest managers rely on studies of how deer impact bird habitats in other regions, especially those with hardwood-dominated understory (e.g., deCalesta 1994, McShea and Rappole 2000), they will underestimate habitat values for understory-dependent species at sites similar to ours.

On balsam fir-dominated understory plots with abundant BTBWs, not only were balsam fir stem densities greater, balsam firs also were taller than other understory species (Table 2). In particular, many (41%) balsam firs were 1–2 m tall, whereas most (66%) of the understory maples were <1 m tall and only 15% were in the 1–2 m category; taller deciduous stems typically showed evidence of being repeatedly browsed (i.e., many short remnants of branches persisted along the main stem). We suggest that this difference in height distribution is likely an important driver of the positive BTBW response to balsam fir at these sites. In addition to nesting in both balsam fir and deciduous cover <1 m tall, BTBWs often nested in the lower branches of balsam firs that were 1–2 m high (LJK and KRH pers. obs.). Furthermore, habitats providing a greater proportion of taller, more structurally complex saplings may provide more cover and foraging substrate for recently fledged young and adult BTBWs (Kolozsvary 2002; LJK, KRH pers. obs.) Although height differences in deciduous understory explained a substantial percentage of the vegetation variability in our study area (Table 1), this was not the focus of our sampling design. Typically, height of deciduous understory is strongly linked to both the intensity of deer browsing and time since the last selection cut or forest thinning, and further research focused on height would likely improve our understanding of habitat use by BTBWs in these forests.

Holmes et al. (1996) found that areas with more understory had greater densities of BTBWs and greater proportions of older birds. The age-ratio pattern in our plots indicated that older birds preferred areas with more balsam firs; however, the ASY:SY age ratio was not significantly greater in balsam fir-dominated plots, although these plots had the greatest densities of BTBWs. In plots where we found BTBWs, 74% were older males; this is at the high end of the range (50–79%) observed by Holmes et al. (1996) in New Hampshire, and is greater than ratios reported by Graves (1997b) for birds in northern Michigan and Ontario (50–60%). It is possible that the relative scarcity of yearling birds on our study sites precluded detection of an association between age and understory characteristics. Return rates also indicated a preference for abundant balsam fir in the understory (mean return rates were 26% in balsam fir-dominated plots and 11% in deciduous-dominated plots, a non-significant difference), but these values were based on only one year of data collected during a single survey per site.

Veery abundance did not increase as balsam fir understory increased, but Veerys were more abundant in plots with dense understory than in those with minimal understory. Veerys use a broader range of nest sites than BTBWs, including on the ground, on downed branches or logs, and in understory vegetation (Moskoff 1995; KRH unpubl. data). In a study by

Heckscher (2004), Veerys generally built their nests where dense vegetation was <1.5 m tall and there was sparse vegetation between 2.5 and 3 m high; this is consistent with our observation that Veerys were more common in sites with dense understory. We observed that Veerys commonly nested in taller firs (2–4 m), indicating that an abundance of taller balsam firs may be important in some stands, but balsam fir density alone does not appear to reliably predict the relative abundance of Veerys. The fact that a few Veerys were found at sites with little understory also suggests that factors we did not measure, such as presence of coarse woody debris, may be useful predictors of Veery abundance in Great Lakes hardwood forests.

Our results indicate that stem density of balsam fir understory predicted BTBW abundance in deer-browsed forests of northern Michigan. The density of small trees, which covaried with balsam fir and total understory density (because both variables reflect time since the last thinning or selective harvest), also predicted BTBW abundance. Balsam fir is a conspicuous plant that is easily mapped and quantified from aerial photographs taken in spring, which could make it a useful, practical indicator of BTBW habitat. Managers seeking to determine the spatial and temporal pattern of harvest activities in hardwood forest (currently, harvest methods for hardwood stands in the Hiawatha National Forest focus on selection cutting) could rank sites based on the prevalence of balsam fir and then stagger the times at which sites containing high densities of balsam fir would be harvested. We recommend that small balsam firs be left in the understory when overstory trees are removed, especially in areas most impacted by deer. Ideally, these activities would be paired with avian population monitoring to verify the effectiveness of using balsam fir density as an indicator of BTBW abundance, and to identify relationships between other songbirds and this plant species.

ACKNOWLEDGMENTS

We thank the following individuals and organizations that helped make this project possible. J. A. Witter, T. L. Root, S. J. Sjogren, and J. A. Craves were essential in enabling us to complete this project. Those who helped with fieldwork included K. S. Sheldon, S. K. Fruchey, H. A. Petrillo, L. K. Peterson, D. Y. Sasaki, G. R. Kearns, L. A. Jacobs, B. J. Dantzer, J. E. Law, G. L. Norwood, and J. J. Segula. C. A. Geddes, S. J. Brines, and R. L. Pickert assisted with GIS analyses. M. A. Kolozsvary collaborated in grant-writing; R. Bowman, B. A. Hahn, M. E. McPhee, and L. A. Riopelle reviewed drafts of this manuscript. Project funding was provided by the Doris Duke Charitable Foundation, U.S. Fish and Wildlife Service, U.S. Department of Agriculture McIntire-Stennis Research Program, Rackham Graduate School at the University of Michigan, and the U.S. Department of Agriculture Forest Service, Hiawatha National Forest.

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The Wilson Journal of Ornithology 118(4):471–477, 2006

SOARING AND GLIDING FLIGHT OF MIGRATING BROAD-WINGED HAWKS: BEHAVIOR IN THE NEARCTIC AND NEOTROPICS COMPARED

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ABSTRACT.—We compared migrating behavior of Broad-winged Hawks (*Buteo platypterus*) at two sites along their migration corridor: Hawk Mountain Sanctuary in eastern Pennsylvania and the Kéköldi Indigenous Reserve in Limón, Costa Rica. We counted the number of times focal birds intermittently flapped their wings and recorded the general flight type (straight-line soaring and gliding on flexed wings versus circle-soaring on fully extended wings). We used a logistic model to evaluate which conditions were good for soaring by calculating the probability of occurrence or absence of wing flaps. Considering that even intermittent flapping is energetically more expensive than pure soaring and gliding flight, we restricted a second analysis to birds that flapped during observations, and used the number of flaps to evaluate factors influencing the cost of migration. Both the occurrence and extent of flapping were greater in Pennsylvania than in Costa Rica, and during periods of straight-line soaring and gliding flight compared with circle-soaring. At both sites, flapping was more likely during rainy weather and early and late in the day compared with the middle of the day. Birds in Costa Rica flew in larger flocks than those in Pennsylvania, and birds flying in large flocks flapped less than those flying alone or in smaller flocks. In Pennsylvania, but not in Costa Rica, the number of flaps was higher when skies were overcast than when skies were clear or partly cloudy. In Costa Rica, but not in Pennsylvania, flapping decreased as temperature increased. Our results indicate that birds migrating in large flocks do so more efficiently than those flying alone and in smaller flocks, and that overall, soaring conditions are better in Costa Rica than in Pennsylvania. We discuss how differences in instantaneous migration costs at the two sites may shift the species' migration strategy from one of time minimization in Pennsylvania to one of energy minimization in Costa Rica. *Received 15 November 2005, accepted 8 July 2006.*

Each year, more than one million Broad-winged Hawks (*Buteo platypterus*) make a round-trip migration of 6,000–10,000 km along the Mesoamerican Land Corridor when traveling between their North American breeding grounds and wintering areas in Central and South America (Bildstein and Zalles 2001). Because the power requirement for continuous, flapping flight has an allometric mass exponent of 1.17 (Pennycuick 1972), large-bodied migrants are penalized compared with small-bodied migrants in that they need a disproportionately larger fat reserve to accomplish a non-stop, powered-flight migration of a given distance. As such, long-distance migration represents a potentially acute energetic challenge for large-bodied migrants such as Broad-winged Hawks (265–560 g; Goodrich et al. 1996). In fact, measures of fat reserves at the onset of migration suggest that Broad-winged Hawks do not carry the fuel supply needed to sustain powered flight between their breeding and wintering grounds without also feeding en route (Bildstein 1999).

There are two possible solutions to this energetic challenge. First, large-bodied migrants may complete their migration in stages, pausing periodically to feed and replenish fat reserves en route. Second, if their flight mechanics permit, they may significantly reduce the energetic costs associated with powered flight by relying instead on soaring and gliding flight. Although ducks, geese, and many shorebirds and landbirds exploit the first strategy (Moore 2000), Broad-winged Hawks do

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not feed substantially when migrating, particularly in the tropics (Bildstein 1999), possibly because their sit-and-wait foraging strategy does not lend itself well to the high capture rates needed for the rapid accumulation of fat reserves. Instead, they rely heavily on gliding and soaring flight to complete their long-distance movements (Smith et al. 1986). Because basal metabolic rate (BMR) increases with mass by an allometric exponent of approximately 0.75, soaring and gliding flight become increasingly cost-efficient as mass increases (Hedenström 1993). Indeed, it has been estimated that 100 g of fat would fuel powered flight for only about 5 days in Broad-winged Hawks, but it would sustain soaring flight in the species for an estimated 20 days (Smith et al. 1986).

Soaring flight is based on the conversion of the energy in atmospheric air currents into primarily potential energy (Pennycuick 1972). In North America, soaring Broad-winged Hawks gain altitude while circling in thermals and riding deflection updrafts with their wings and tails fully spread, and then gliding on flexed wings along their preferred direction of travel as they convert the altitude gained into distance traveled while seeking the next thermal or updraft along their migratory route (Kerlinger 1989). In Central America, where the species also alternately soars and glides among small thermals, it also straight-line soars and glides in the much larger tropical thermals and "thermal streets" (*sensu* Smith 1985) found in that region.

Because the distribution, abundance, and strength of thermals and updrafts are affected by topography, vegetation cover, vertical temperature gradient of the atmosphere, and intensity of solar radiation, soaring flight imposes constraints on the spatial and temporal organization of migration (Kerlinger 1989). Soaring migrants are able to migrate efficiently only when sufficient solar radiation and low cloud cover favor the production of thermals, thus concentrating individuals in specific seasonal and daily time windows. Also, in the temperate zone, thermals often occur in small, localized pockets, which sometimes force soaring birds to fly close to each other when using the same thermal. This has led some to suggest that flocking behavior occurs passively among soaring migrants, as limited spatial and temporal windows of soaring opportunity act to group the birds during their migrations (Smith 1985). Alternatively, others have speculated that soaring migrants, such as Broad-winged Hawks, actively form groups because doing so allows them to gather information (e.g., Danchin et al. 2004) about the location and strength of individual thermals passively provided by individuals traveling with them (Kerlinger 1989).

As Broad-winged Hawks travel south in autumn, it is likely that they adjust their flight behavior to accommodate changes in the abundance and strength of the thermals they encounter. At the onset of migration in late summer in the temperate zone, the sun's height in the sky and overall solar intensity begin to decline (Bildstein 1999); the strongest and greatest abundance of thermals tends to occur episodically during the several days of fair weather that typically follow the passage of cold fronts (Allen et al. 1996). Farther south in the tropics, the sun's height in the sky and solar intensity remain relatively more constant during the migration period and thermal strength appears to vary primarily as a function of local cloud cover (Smith 1980).

It has been suggested that the movements of soaring migrants are less constrained in the tropics than in the temperate zone and that their flight patterns differ in the two regions (Bildstein and Saborio 2000). For example, Fuller et al. (1998) reported that the migration speed of satellite-tracked Swainson's Hawks (*Buteo swainsoni*) soaring and gliding between breeding grounds in western North America and wintering areas in Argentina was 42% greater in the tropics than in the temperate zone. Here, we compare the flight behavior of Broad-winged Hawks at temperate and tropical sites to test three main predictions: (1) because soaring conditions are better in the tropics, birds would begin flying earlier in the day and flap less there than in the temperate zone; (2) birds within a given site would flap less at higher temperatures and less cloud cover; and (3) birds would flap less when traveling in large flocks than when traveling alone or in smaller flocks.

METHODS

We observed migrating Broad-winged Hawks in the temperate zone at Hawk Mountain Sanctuary in the Central Appalachian Mountains of eastern Pennsylvania (40° 58′ N, 74° 59′ W; 464 m ASL) on 10–28 September 2002, during peak passage at that site. Hawk Mountain straddles the 300-km-long Kittatinny Ridge, which acts as a leading line for raptor migrants in the region (Bildstein 1999). In the tropics, we observed migrating Broad-winged Hawks from a 10-m tower at the Kéköldi Indigenous Reserve, southeast of Puerto Viejo in Talamanca, Limón, Costa Rica (9° 38′ N, 82° 47′ W; 200 m ASL) on 2–19 October 2002, during peak passage at that site (Porras-Penaranda et al. 2004). The Caribbean Sea, ~2 km to the north, and the Talamanca Mountains, ~5 km to the south, funnel birds through the region's coastal lowlands, making this area one of several major concentration points along the Mesoamerican Land Corridor (Bildstein and Zalles 2001).

We used 7 × 35 binoculars and a 20–60× zoom telescope to watch birds at each site between sunrise and 18:00 EST. Individual observations were made on a focal individual during a 30-sec sample period beginning as soon as the bird was identified as a Broad-winged Hawk. The 30-sec length represented a fair trade-off between gaining a representative record of flight behavior and losing contact with the focal bird before the observation period was completed. During our observations, we recorded the number of seconds the focal individual spent (1) circle-soaring in an individual thermal and (2) straight-line soaring and gliding between thermals and along thermal streets. When circle-soaring, birds ascended thermals on fully outstretched wings with their tails fanned. When straight-line soaring and gliding, birds flew on semi-flexed wings with their wingtips and tails partly folded. We also recorded the number of flaps (i.e., individual wing beats) and used it as a measure of powered flight.

We determined flock size by counting or estimating the number of birds soaring within the same thermal or soaring and gliding in the same flight line as the focal bird. In Pennsylvania, flocks were composed of only Broad-winged Hawks. In Costa Rica, however, Broad-winged Hawks sometimes commingled with Swainson's Hawks and Turkey Vultures (*Cathartes aura*) in mixed-species flocks. We noted temperature and cloud cover (clear and partly cloudy skies versus complete overcast) at hourly intervals. We also noted time of day as time after sunrise (06:45 EST in Pennsylvania and 05:25 CST in Costa Rica) and then divided the day into three periods (early, mid, and late) to simplify analyses. At both sites, the early period included the first 4 hr after sunrise, the mid-period the next 4 hr, and the late period the next 3 hr. We did not record flight behavior later in the day.

We performed all analyses using the JMP 5.0.1 statistical package (SAS Institute, Inc. 2002). We used non-parametric Mann-Whitney *U*-tests to compare mean onset of activity and flock size between Pennsylvania and Costa Rica. To allow comparisons between soaring and gliding phases of flight, we restricted our analyses to 30-sec sequences in which the focal bird remained in one flight phase (soaring or gliding). We conducted two general analyses. The first examined which conditions enabled soaring and gliding flight without flaps. The second examined factors that influenced the extent of flapping when it did occur.

For the first analysis, we divided observations into those during which the bird did or did not flap. We ran a stepwise logistic regression that included all independent variables (site, flight phase, flock size, temperature, and cloud cover) and two-way interactions. The odds ratio (OR) measures how the fitted probability is multiplied as the regressor changes from its minimum to its maximum for continuous data, or from one category to the other for nominal data (Hosmer and Lemeshow 1989). We used the log-likelihood ratio (L-R) test to determine *P*-values. The second analysis was restricted to birds that flapped at least once while we were observing them. For each site, we conducted an ANCOVA on the number ($\log_{10}$-transformed) of flaps, according to the flock size, flight phase, temperature, and cloud cover. Data are presented as means ± SE.

RESULTS

We made 1,537 30-sec observations of Broad-winged Hawks during 13 days in Pennsylvania and 2,103 observations during 15 days in Costa Rica. In Costa Rica, flocks ranged in size from 2 to >1,000 individuals (mean = 427 ± 10; median = 140). In Pennsylvania, flock size never exceeded 350 indi-

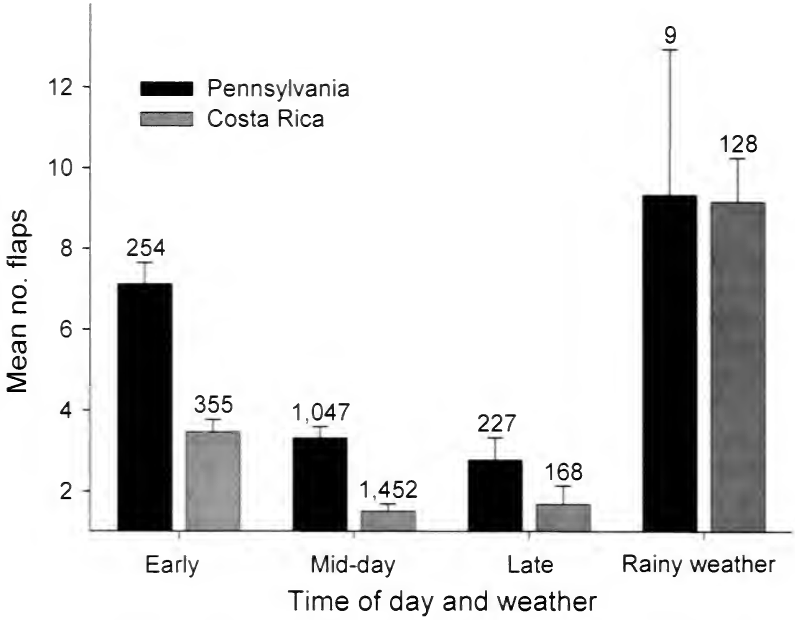

FIG. 1. Mean numbers of wing flaps per 30-sec observation period (±SE) in relation to time of day and rain condition in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002. Numbers above the error bars represent sample sizes.

viduals (mean = 26 ± 1; median = 10). Overall, flock size was significantly greater in Costa Rica than in Pennsylvania (U = 1177.6, $P < 0.001$). The first migrant of the day was sighted almost one hour later in Pennsylvania than in Costa Rica (198 ± 53 min after sunrise versus 150 ± 11 min after sunrise, U = 6.32, $P = 0.022$), and the first individuals sighted each day were more likely to flap in Pennsylvania than in Costa Rica (35% versus 16%, L-R $\chi^2 = 162.7$, $P < 0.001$).

TABLE 1. Results of the logistics model for the occurrence of flapping flight among Broad-winged Hawks in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002, by temperature (°C), flock size, flight type (circle or straight-line soaring), and cloud cover (overcast or not). The log-likelihood (L-R) χ^2 and P-value are shown. Sample size is 2,153.

Term	df	L-R χ^2	P
Site	1	10.24	<0.001
Temperature	1	111.56	<0.001
Site × temperature	1	55.13	<0.001
Flock size	1	16.76	<0.001
Flight type	1	77.63	<0.001
Cloud cover	1	15.24	<0.001

At both sites, birds were more likely to flap early and late in the day than at mid-day (Pennsylvania: L-R $\chi^2 = 67.1$, $P < 0.001$; Costa Rica: L-R $\chi^2 = 68.6$, $P < 0.001$; Fig. 1). Flapping was greater during rainy periods at both sites, but significantly so only in Costa Rica (Pennsylvannia: L-R $\chi^2 = 3.84$, $P = 0.051$; Costa Rica: L-R $\chi^2 = 78.6$, $P < 0.001$). To account for these effects, we excluded from the analyses that follow any observations made early and late in the day and during rainy weather.

The logistic model indicated which conditions favored soaring flight (Table 1) and the ANCOVA identified which factors determined the extent of powered flight when it occurred (Table 2). Both extent and probability of flapping were greater during straight-line soaring and gliding than during circle-soaring (Fig. 2; OR = 0.3). The overall flapping probability was lower when birds flew in larger flocks than in smaller flocks or alone (OR = 2.8). There was no significant difference between flapping rates in Pennsylvania and Costa Rica when birds flew in flocks of up to 50 birds (L-R $\chi^2 = 3.75$, n = 1,038, df = 1, $P = 0.053$); however, when birds were in flocks

TABLE 2. Comparisons of factors influencing the numbers of flaps per observation of Broad-winged Hawks in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002. The ANCOVA was restricted to birds that flapped at least once during the observation.

		Pennsylvania (n = 208)		Costa Rica (n = 156)	
	df	F-ratio	P	F-ratio	P
Flock	1	0.10	0.76	9.17	0.003
Flight type	1	14.20	<0.001	18.63	<0.001
Temperature	1	1.42	0.24	8.34	0.005
Cloud cover	4	3.29	0.012	1.70	0.16

that ranged in size from 51 to 350 birds, flapping probability was significantly lower in Costa Rica than it was in Pennsylvania (L-R χ^2 = 10.25, n = 468, df = 1, P = 0.001). More than 94% of the Broad-winged Hawks seen in Costa Rica were flying in flocks of ≥50, and flapping was far more likely in Pennsylvania than it was in Costa Rica (OR = 1.87; Fig. 2). Moreover, the number of flaps decreased with flock size in Costa Rica, but not in Pennsylvania (Table 2).

Overall, the probability of flapping was greater during periods of complete overcast than it was when cloud cover was ≤75% (OR = 1.7); however, cloud cover had an effect on the number of flaps only in Pennsylvania (Table 2). Although probability of flapping decreased as temperature increased (minimum temperature = 15° C, maximum temperature = 31° C, OR = 574.1); the relationship was significantly weaker in Pennsylvania than in Costa Rica (site × temperature interaction term, OR = 0.03). Accordingly, temperature had an effect on the number of flaps in Costa Rica but not in Pennsylvania (Table 2).

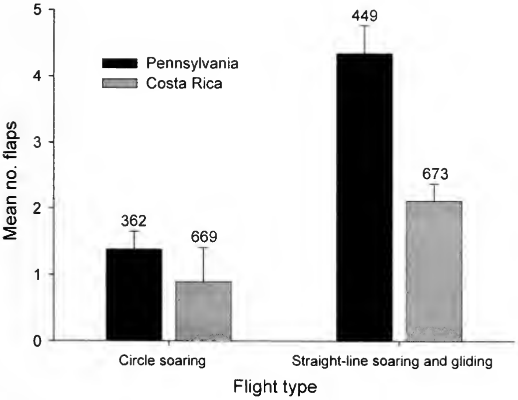

FIG. 2. Mean number of wing flaps per 30-sec observation period (± SE) made by Broad-winged Hawks in circle soaring or straight-line soaring and gliding flight in Pennsylvania, USA, 10–28 September 2002, and in Talamanca, Costa Rica, 2–19 October 2002. Numbers above the error bars represent sample sizes.

DISCUSSION

Since Huffaker (1897) first provided evidence of the existence of thermal updrafts based on observations of soaring birds, many studies have shown that avian flight can be used to gather information on meteorological processes (Shannon et al. 2002). We present our data as a biological method for measuring soaring conditions for Broad-winged Hawks traveling between the temperate zone and the tropics during southbound migration in autumn, and we offer a preliminary indication of how differences in soaring conditions affect the efficacy of migratory flight in the species.

In general, our observations confirm the flight behavior of soaring migrants documented elsewhere (Kerlinger and Gauthreaux 1985, Spaar and Bruderer 1997, Spaar et al. 1998). For example, as temperatures and solar radiation increase each morning, birds rely less on flapping flight and more on soaring and gliding flight, presumably to reduce the energetic costs of travel by taking advantage of the stronger mid-day thermals.

The negative correlation between flapping rates and flock size suggests that Broad-winged Hawks use information available in flocks to increase their flight efficiency (Kerlinger 1989). That said, although smaller flock sizes and higher flapping rates in Pennsylvania were probably due at least in part to this effect, smaller and weaker thermals in Pennsylvania also may have contributed to a greater likelihood of flapping at the site.

We suggest that migrating Broad-winged Hawks do not pursue a pure soaring and gliding strategy throughout their migration because they are constrained from doing so in two ways. First, they cannot soar when vertical airspeeds within thermals fail to reach a critical threshold value, and second, they cannot glide efficiently when inter-thermal distances exceed their maximum gliding range (Kerlinger 1989). Our data indicate that Broad-winged Hawks respond to these constraints by using powered flight preferentially during straight-line soaring and gliding flight and secondarily when circle-soaring. This tactic also has been observed in migrating Common Cranes (*Grus grus*; Pennycuick et al. 1979), as well as in other raptor species. By stretching inter-thermal glides with flapping flight, birds increase the distance realized, thereby extending their ability to reach and use the next thermal (Pennycuick 1998). Second, under certain circumstances, soaring and gliding can slow travel compared with flapping flight, particularly when the birds are soaring in small thermals. Indeed, migrants are likely to pursue a pure soaring strategy only when they have time to wait for the proper conditions and are able to move slowly along the migration corridor. For Broad-winged Hawks, time limitations may be more important in Pennsylvania than in Costa Rica, because solar intensity and photoperiod decrease rapidly during September in Pennsylvania, thereby forcing birds to move south in a brief window of time (Bildstein 1999). On the other hand, solar intensity and photoperiod remain relatively high and constant year-round in Costa Rica, resulting in a more prolonged window of time for hawk movements (Porras-Penaranda et al. 2004).

As a result, Broad-winged Hawks may be more likely to use a time-minimization strategy in temperate than in tropical zones, resulting in a higher flapping rate in Pennsylvania. Assuming an energy consumption of approximately 4 × BMR in soaring flight and a climbing rate of 1 m/sec, flight theory predicts that during time-minimizing migration, heavy birds (>132 g) should switch from soaring to flapping flight (Hedenström 1993). For energy-minimizing migration, the switch from soaring to flapping flight occurs at a lower climbing rate. Thus, as the rate of climbing decreases, time-minimizing migrants should switch from soaring to flapping flight sooner than energy-minimizing migrants (Hedenström 1993). These temporal and energetic aspects may explain why Broad-winged Hawks are more likely to resort to flapping in Pennsylvania than in Costa Rica.

Our observations indicate that Broad-winged Hawks shift from a mixed strategy of soaring and gliding supplemented by powered flight to a nearly pure strategy of soaring and gliding as they proceed during their southbound migrations, suggesting that the instantaneous metabolic cost of migration declines from north to south. By relying more on powered flight in the north, where conditions are less favorable for soaring, Broad-winged Hawks may trade off energy against time, a phenomenon also observed in Levant Sparrowhawks (*Accipiter brevipes*; Spaar et al. 1998). This would allow them to move along the corridor at a faster rate at the expense of depleting fat reserves.

Finally, we highlight the fact that we did not discriminate adult from juvenile Broad-winged Hawks, and that we observed migrants at only two sites. Additional observations in which the flight behavior of adults and juveniles are compared and in which other species are observed at other temperate and tropical sites are likely to provide important insights into the extent to which age and latitudinal geography affects the flight behavior of migrating birds of prey.

ACKNOWLEDGMENTS

This study was conducted as part of VC and JFT's undergraduate research project at the Université de Sherbrooke and when VC and JFT were Conservation Science Interns at Hawk Mountain Sanctuary (supported by foreign studies scholarships from the Ministère de l'Éducation du Québec). We thank the autumn 2002 interns at Hawk Mountain Sanctuary and the interns and Bribri people at Kéköldi Indigenous Reserve for their assistance and hospitality. Finally, we are grateful to R. Spaar, P. Kerlinger, C. J. Farmer, and three anonymous referees for helping us improve our manuscript. This is Hawk Mountain Sanctuary Contribution to Conservation Science, number 135.

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COLONIALITY, MATE RETENTION, AND NEST-SITE CHARACTERISTICS IN THE SEMIPALMATED SANDPIPER

JOSEPH R. JEHL, JR.[1]

ABSTRACT.—Coloniality is unusual among Scolopacidae. At Churchill, Manitoba, however, the small, remnant population of Semipalmated Sandpipers (*Calidris pusilla*) is highly clumped, with nesting density approximating 3–4 pairs/ha, and should be considered colonial. The species exhibits high fidelity to territory, mates, and nest sites—behaviors that promote rapid pair formation and allow experienced birds to increase their reproductive success by nesting earlier than pairs forming for the first time. The value of experience and early nesting was evidenced by the fact that six of seven returning young were produced by experienced pairs and had hatched on the first day of their respective nesting seasons. Nests were placed in dry locations very near open water. Those adjacent to small shrubs had slightly greater success, and young produced from these nests had much higher rates of return than those from nests placed amid sedges. In other parts of their breeding range, Semipalmated Sandpipers are also clumped and seem likely to be colonial. If so, estimates of breeding populations derived from indirect methods, such as habitat assessment from aerial photographs, will have limited applicability and will need to be complemented by ground-truthing. *Received 3 October 2005, accepted 2 May 2006.*

Spatial distribution in breeding birds runs the gamut from solitary nesting coupled with strongly developed territorial behavior to highly colonial, with the defended area being limited to the area that parents can protect without leaving their nests. Shorebirds (Charadrii) exhibit similar variation. Most are solitary nesters, but in some groups (e.g., Dromadidae, Recurvirostridae, Glareolinae) coloniality is the rule, the extreme being attained by the Banded Stilt (*Cladorhynchus leucocephalus*), in which densities up to 18 nests/m^2 have been reported (Minton et al. 1995, del Hoyo et al. 1996, van Gils and Wiersma 1996). Lacking "objective (or even widely accepted) criteria as to how clumped nests must be to constitute a true colony," ornithologists have used such terms as "semicolonial," "strongly clumped," or "loose colony" to describe situations in which "rather more dispersed nests . . . are . . . judged to be in a clump relative to the density of nests in the general vicinity" (Campbell and Lack 1985: 95). In any case, the essence of coloniality is that birds of a feather are disposed to nest near each other, the attraction being primarily social rather than to a common habitat.

Among Scolopacidae, coloniality of any kind is rare, and in the calidridine sandpipers (Calidridini) "semi-coloniality" has been reported or suspected only in the Western (*Calidris mauri*) and Broad-billed (*Limicola falcinellus*) sandpipers (Palmer 1967, van Gils and Wiersma 1996). To this small list may be added the Semipalmated Sandpiper (*Calidris pusilla*), a monogamous and highly territorial species that breeds in the Subarctic and lower latitudes of the North American Arctic. Despite having been studied in only a few areas, its breeding biology is well-documented, mainly through comprehensive studies at La Pérouse Bay, Manitoba, by Gratto-Trevor (1992, and references therein). Although known to nest at relatively high densities, the Semipalmated Sandpiper has not been suspected of nesting colonially. At Churchill, Manitoba, however, that appears to be the case. Here I present observations on Semipalmated Sandpiper spacing and nesting behavior, along with information on nest-site characteristics, philopatry, and other aspects of the species' breeding biology that complement and extend Gratto-Trevor's findings.

METHODS

Observations were made in a potential nesting area of 7,000 ha in the "immediate Churchill Area" (Jehl and Lin 2001, map in Jehl 2004: 58° 45′ N, 94° 00′ W) from 1993 through 2004 as part of a broader study on shorebird biology (Jehl and Lin 2001, Jehl 2004). From previous studies in 1964 through 1967, I was familiar with the status of shorebirds in the Churchill area (Jehl and Smith 1970). When I resumed studies in 1991, I

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failed to encounter Semipalmated Sandpipers until 1993, when I found a few pairs nesting in a small meadow (~25 ha) 25 km east of the Churchill townsite. Then, and in each subsequent year, I attempted to find all nests and mark all individuals. I trapped adults at the nest in a simple walk-in trap and banded them with aluminum bands (or stainless steel, when available) and individually coded colored plastic bands. I made standard measurements with dial calipers (culmen and tarsus to 0.1 mm; flattened wing to 1 mm) and weighed each bird on a digital scale (to 0.1 g). Chicks were banded (but not color-marked) before they left the nest. From this effort, the identities of most adults (88% of 93 from 1993 to 2001) and young (73% of 120 from 1993 to 2000) were known, which allowed their status, mates, distribution, and nesting success to be followed from year to year. I aged adults on the basis of Gratto and Morrison's (1981) observation that most first-year birds are distinguishable from older birds by having up to four newly replaced outer primaries. Observations in 2001 through 2004 focused on documenting the identities of returned birds.

In most calidridines, males are typically smaller (e.g., Jehl and Murray 1985), but there is much overlap. To determine sex, I also used behavioral information, including observations that males defend territories much more strongly, sing longer and more complex songs, and are bolder around the nest. For birds returning in subsequent years, it was usually possible to use behavior to test earlier determinations: in only 2 of 25 cases did a tentative sexing need to be reconsidered.

RESULTS

Phenology and colony designation.—Semipalmated Sandpipers migrate through the Churchill region between the last days of May and the first third of June. Locally nesting birds move immediately to breeding areas, where they engage in prolonged and conspicuous territorial and courtship displays. Display flights take place at elevations of 40–50 m and may last 10 min or more. Typically, these displays involve several birds, which chase back and forth over, and well beyond, the nesting area.

From 1993 through 2004, the only Semipalmated Sandpipers nesting in the potential (7,000 ha) nesting area occurred in the 25-ha meadow described above. Bordered by two lakes and dotted with shallow ponds that dried out by late June, the area was relatively wet and contained slightly more shrubby vegetation than some other nearby sites. Because (1) the nesting area occupied only 3–4 ha of this meadow, (2) nest density was extremely high (see below), (3) similar habitat elsewhere in the Churchill area was unused, (4) the historic distribution of Semipalmated Sandpipers at Churchill had not been limited to this type of habitat, and (5) nesting areas used through the 1960s, though largely unchanged, were no longer used, it was clear that the birds were attracted to each other and not to any specific habitat or topographic conditions. Consequently, their nesting behavior could be described as colonial. Elsewhere in the Churchill area, I encountered Semipalmated Sandpipers only twice from 1993 through 2004: one unmated male, and an apparent pair, each located >5 km from the colony. All three birds disappeared after a few days.

The colony contained five pairs in 1993. Colony size had increased slightly by 1995 (11 nests; Table 1) and (probably) 1996, but runoff in 1996 flooded some early nests and may have prevented some pairs from finding suitable territories or renesting. In 1997, the number of adults was halved and I found only two nests. Subsequently, through 2001, the colony size fluctuated from two to three pairs, and by 2003 (and perhaps 2004) there was only a single, unpaired male. At maximum size in 1995 (Fig. 1), the colony encompassed 3.4 ha (determined by a polygon drawn around the outermost nests; this area included open-water areas where nesting was impossible), had a maximum linear extent of 416 m, and a density of 3.2 pairs/ha (maximum = 4.1 in 1993). Nests were tightly packed, the nearest-neighbor distance averaging about 55 m (minimum = 31 m).

Mate fidelity.—As in some other calidridines (e.g., Least Sandpiper, *Calidris minutilla*; Stilt Sandpiper, *C. himantopus*; Dunlin, *C. alpina*; Jehl 1970; JRJ unpubl. data), Semipalmated Sandpipers form long-term bonds and pairs tend to re-occupy former territories as long as both members are alive (see also Gratto et al. 1985). In 16 cases in this study, both partners returned, pairs reunited 13 times in the follow-

TABLE 1. Population size and density of Semipalmated Sandpipers at Churchill, Manitoba, 1993–2001.

Year	Population size[a]	No. nests	Nesting area (ha)[c]	No. pairs/ha[c]	Maximum extent of colony (m)	Distance to nearest nest(s): [range] and median (m)
1993	≥10	5	1.2	4.1	126	[54–181] 87.3
1994	16–19	8	2.8	2.9	268	[52–63] 55.1
1995	22–24	11	3.4	3.2	416	[31–101] 54.4
1996	21–22	8[b]	2.7	2.9	381	[37–124] 88.4
1997	12	2	—	—	121	121
1998	7	3	—	—	274	[84–193]
1999	4	2	—	—	—	55
2000	6–8	3	—	—	—	90, 91
2001	≥6	3	—	—	—	—

[a] Estimated number of adults in colony early in the season.
[b] Omits one renesting.
[c] Could not be calculated from two points or when nests were arranged linearly.

ing season, and all had nested successfully in the previous year. Three pairs divorced (one previously successful, two unsuccessful). The successful male acquired a new mate and his old mate soon disappeared. Of the two previously unsuccessful pairs, the nest of one was flooded, the female acquired a new mate, and the old male skipped breeding; both birds of the other pair acquired new partners, but the males retained their previous nest sites. Of the pairs that reunited, two remained intact for four seasons, three for three seasons, and two for two seasons.

Nineteen pairs failed to reunite. The reasons can only be guessed, as banded but unidentified birds occasionally showed up early in the

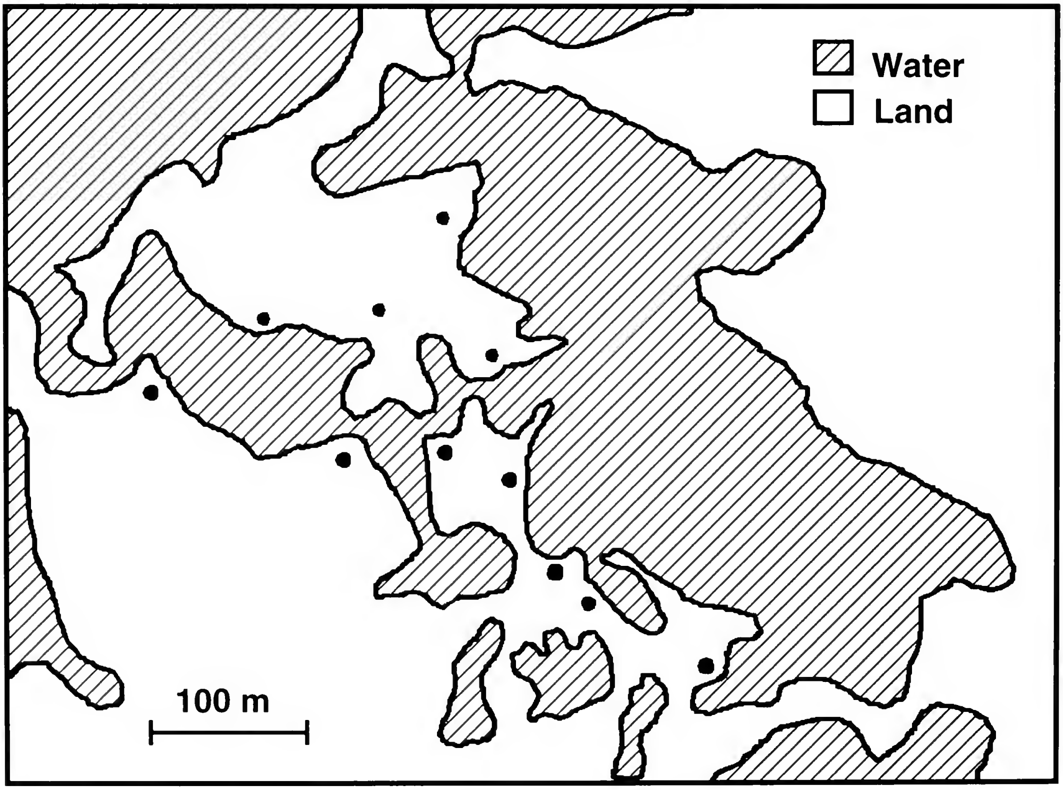

FIG. 1. Location and spacing of Semipalmated Sandpiper nests (●) at Churchill, Manitoba, 1995.

TABLE 2. Spacing and dispersal of Semipalmated Sandpipers at Churchill and La Pérouse Bay, Manitoba.

	Churchill 1993–2001		La Pérouse Bay 1980–1984[a]	
Variable	*n*	Spacing, behavior	*n*	Spacing, behavior
Size of breeding area; habitat		3–4 ha; a single small meadow		2 km^2; on delta of Mast River
Population size; density		2–11 pairs; 3–4/ha		100 pairs; 1/ha
Pairs reuniting, if both alive	16	13 (81%)	79	64 (81%)
Reuse of old nest cup	41	8 (19.5%)	305	13 (4.3%)
Rate of nest reuse if both parents returned	13	8 (61.5%)		No data
Nest shift: reunited pairs	14	Range = 0–85 m; mean = 25.4 ± 36 m; mode = 0 m	168	Range = 0–575 m; annual medians: 40–66 m
Nest shift: female mate change	8	4–360 m, mean = 153 ± 126 m; median = 115m	33	Range = 23–825 m; annual medians: 138–174 m

[a] From Gratto et al. (1985).

year and then disappeared, perhaps without mating or perhaps because their nest was lost before I could find it. In several cases, the break-up was evidently due to bad timing (one partner returned late) or the unavailability of a previous nest site (see below).

Nest-site selection and site tenacity.—Just as Semipalmated Sandpipers tend to retain mates and territories from year to year, they also retain nest sites, as long as the previous nesting attempt was successful, the mate remains alive, and the nest is in suitable condition and does not contain unhatched eggs from the previous season. Of 13 cases in which both mates returned and reunited, the distance to subsequent nests ranged from 0 to 85 m (mode = 0 m; Table 2). One pair used the same nest for 4 successive years.

Semipalmated Sandpipers selected nest locations very near ponds (mean = 10.9 m ± 8.8, range = 0.5–29.5 m, *n* = 26), but placed their nests in dry situations on the sides or tops of small hummocks or ridges. Two types of nest sites were used: "shrub" sites were located under, or adjacent to, small bushes—in this case sweetgale (*Myrica gale*) or dwarf birch (*Betula nana*)—which typically allowed access from only one direction; "sedge" sites were in low, damp areas and nests were placed in a clump of sedge (*Carex* spp.). At 41 documented sites (including those reused by the same pair in subsequent years), 30 were in shrub and 11 in sedge. Nesting success was slightly (but not significantly) greater in shrub sites (83% versus 72%), which are better concealed and less subject to flooding. However, the greater desirability of shrub sites was clear from their retention rates. Of 25 successful shrub sites, 14 (56%) were reused, 13 by a returning pair and 1 by a male with a new mate. Of the 11 successful shrub sites that were not reused, the nest cup or habitat had become unusable (*n* = 3) or one or both mates failed to return (*n* = 8). In sedge sites, 8 of 11 nestings were successful, yet none was reoccupied (1 site was used several years later by a pair with no previous breeding experience; the nest failed). In the other cases, the habitat had changed over the intervening winter (*n* = 3) or one or both mates failed to return (*n* = 4).

Among individuals that moved to a new location, males (*n* = 9) tended to stay near their previous nest site (median distance = 40 m). Eight paired with females that had no previous experience, and one bred successfully in the same territory for 4 successive years, each time with a new mate and each time moving ~50 m away from the previous site before returning to the original nest in the 4th year. Females (*n* = 8) tended to move farther away from previous nest sites (median = 115 m). Three females paired with experienced males that held territories near the center of the colony; one of these birds failed to nest one year when her nest was flooded, but she returned to her old territory (by then held by a different male) and nested within 4 m of the original scrape. The other five females bred with inexperienced males, whose nests in all but one case were on the periphery of the colony. One pair in its 2nd year moved 60 m, then 80 m in year 3, and 80 m again in year 4. When the nest was flooded in year 4, the birds moved 85 m, which brought them to within 4 m of their original nest.

Of 120 local chicks banded, 7 returned to breed. At least six of these were produced by pairs in which at least one parent had nested successfully in a previous year; five (including two from the same clutch) were produced by two pairs. All returning young paired with inexperienced mates; the males (n = 5) moved 130–225 m (mean = 197 m) and the females (n = 2) moved 85 and 226 m from their natal sites. When the colony was relatively large, young males, with one exception, were only able to obtain territories at the colony edge. One bred on the periphery in his 1st year and then moved to a more central site in his 2nd year. Another male obtained a central location at first breeding, but only after experienced neighbors had reduced territory defense (cf. Jehl 1973) and started incubating; its young hatched a week later than those of other pairs.

DISCUSSION

Breeding behavior.—The aspects of mate and territory retention, philopatry, and dispersal treated in this study largely conform to those reported by Gratto et al. (1985) at La Pérouse Bay, ~30 km to the east (Table 2). At Churchill, nest density was greater than it was at La Pérouse Bay (3–4 versus 1 pair/ha), returning pairs dispersed much less (if at all) from previous nests, and reuse of the nest cup was greater (19.5% versus 4.3%; 61.5% [this study] if both pair members returned). These differences were probably related to topography and the size and stability of the respective nesting areas. Churchill birds were restricted to a small meadow, whereas Semipalmated Sandpipers at La Pérouse Bay bred on a river delta that often experienced high flows during runoff, resulting in greater loss of old nest cups. At Churchill, young males tended to breed at the colony's edge but did not disperse as far from their natal sites as they did at La Pérouse Bay (197 m versus 549 m, respectively), probably because the colony was much smaller.

For any species, the timing of breeding is critical to reproductive success (Lack 1968), and it is widely acknowledged that individuals nesting earlier—nearly always experienced birds—typically have greater success than those that start later (e.g., Soikkeli 1967, Jehl 1970, Gratto et al. 1983, Black 1996, Handel and Gill 2000, Ruthrauff and McCaffery 2005). Early breeding is enhanced by high rates of territory, mate, and nest-site retention, which allow mates to begin nesting as soon as habitat conditions permit. These behaviors are especially important where breeding seasons are short, so it is not surprising that they have been reported in a variety of shorebirds that nest in the Arctic, including Dunlin, Least and Stilt sandpipers, and Black Turnstone (*Arenaria melanocephala*; Soikkeli 1967; Jehl 1970, 1973; Gratto et al. 1985; Jönsson 1987; Handel and Gill 2000; Sandercock et al. 2005; JRJ unpubl. data). In this study the importance of adult experience and early nesting was confirmed by the observation that six of the seven chicks that returned to nest were not only produced by experienced parents but also hatched on the 1st day of their respective hatching periods. The one exception hatched from the penultimate nest of its season and was produced by a pair that had not nested together previously. Although the female had no known experience, the male had bred successfully twice. Whereas the experience of both parents is surely relevant, that of the male is paramount because in this species and many other sandpipers, he takes the sole or major role in rearing the chicks from hatching to fledging (Jehl 1973, Gratto-Trevor 1991; JRJ unpubl. data).

Territory function and spacing.—When not incubating, Semipalmated Sandpipers left their territories and departed the colony area. Some moved to the mudflats of Hudson Bay, a minimum distance of 2–3 km, whereas when water levels were low inland, several might have fed together on mudflats in a lake bordering the colony. Because territory in this species is not based on food availability, it appears that nest spacing is determined by a balance between attraction to conspecifics and the need to maintain sufficient distance between neighbors to prevent predators from finding nests.

Density and population estimates.—Semipalmated Sandpipers are reported to nest at greater densities than other sandpipers, except perhaps the Western Sandpiper. On the North Slope of Alaska, where the Semipalmated

Sandpiper is abundant, Cotter and Andres (2000) reported mean densities of 30 pairs/km^2; farther inland they noted up to 21.3 nests/km^2. At La Pérouse Bay, Manitoba, Gratto et al. (1985) estimated territory size to be 1.0 ha, including defended water areas (maximum density was 2.3 pairs/ha, based on dry land areas). At Churchill, density was even greater, reaching up to 4 pairs/ha (= 400 pairs/km^2, inclusive of pond areas). While all populations of Semipalmated Sandpipers do not necessarily have the same nesting habits (e.g., Gratto and Cooke 1987), spacing is also clumped in the three breeding localities closest to Churchill: Gordon Point and Fox Island (Jehl 2004; JRJ unpubl. data) and La Pérouse Bay (C. Gratto-Trevor pers. comm.). This and the high densities reported elsewhere suggest that the species is probably colonial throughout its range. If so, estimates of breeding populations derived from indirect methods, such as habitat assessment from satellite photography or vegetation maps (e.g., Gratto-Trevor 1996), will have limited applicability. Additional documentation of the kinds of breeding behavior reported in this paper, complemented by ground-truthing of nest spacing in different geographic regions, will be useful.

ACKNOWLEDGMENTS

I was assisted in the field by J. Klima, W. Lin, J. Terp, C. MacDonald, and many volunteers associated with the Churchill Northern Studies Centre. S. I. Bond prepared the map in Figure 1 and helped compile the data. I am grateful to C. Gratto-Trevor for laying the groundwork for this study and to her, J. Klima, A. Henry, and R. I. G. Morrison for insightful comments on this manuscript.

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The Wilson Journal of Ornithology 118(4):485–493, 2006

EFFECTS OF HUMAN RECREATION ON THE INCUBATION BEHAVIOR OF AMERICAN OYSTERCATCHERS

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ABSTRACT.—Human recreational disturbance and its effects on wildlife demographics and behavior is an increasingly important area of research. We monitored the nesting success of American Oystercatchers (*Haematopus palliatus*) in coastal North Carolina in 2002 and 2003. We also used video monitoring at nests to measure the response of incubating birds to human recreation. We counted the number of trips per hour made by adult birds to and from the nest, and we calculated the percent time that adults spent incubating. We asked whether human recreational activities (truck, all-terrain vehicle [ATV], and pedestrian traffic) were correlated with parental behavioral patterns. Eleven *a priori* models of nest survival and behavioral covariates were evaluated using Akaike's Information Criterion (AIC) to see whether incubation behavior influenced nest survival. Factors associated with birds leaving their nests ($n = 548$) included ATV traffic (25%), truck traffic (17%), pedestrian traffic (4%), aggression with neighboring oystercatchers or paired birds exchanging incubation duties (26%), airplane traffic (1%) and unknown factors (29%). ATV traffic was positively associated with the rate of trips to and away from the nest ($\beta_1 = 0.749$, $P < 0.001$) and negatively correlated with percent time spent incubating ($\beta_1 = -0.037$, $P = 0.025$). Other forms of human recreation apparently had little effect on incubation behaviors. Nest survival models incorporating the frequency of trips by adults to and from the nest, and the percentage of time adults spent incubating, were somewhat supported in the AIC analyses. A low frequency of trips to and from the nest and, counter to expectations, low percent time spent incubating were associated with higher daily nest survival rates. These data suggest that changes in incubation behavior might be one mechanism by which human recreation affects the reproductive success of American Oystercatchers. *Received 28 July 2005, accepted 24 April 2006.*

The effect of human recreational activity on wildlife is an increasingly important area of research (Burger 1981, Burger and Gochfeld 1998, Fitzpatrick and Bouchez 1998, Whittaker and Knight 1998, Carney and Sydeman 1999). Human disturbance has been linked to altered foraging behavior (Burger 1981, Burger and Gochfeld 1998, Fitzpatrick and Bouchez 1998, Rodgers and Schwikert 2003, Stolen 2003) and diminished reproductive success of many waterbird species (Hunt 1972, Robert and Ralph 1975, Tremblay and Ellison 1979, Safina and Burger 1983, Rhulen et al. 2003). The mechanisms by which human disturbance lowers reproductive success, however, are poorly understood.

Current data indicate that American Oystercatcher (*Haematopus palliatus*) populations in the Mid-Atlantic states are declining (Mawhinney and Bennedict 1999, Davis et al. 2001). The U.S. Shorebird Conservation Plan lists the American Oystercatcher as a "Species of High Concern," due, in part, to human encroachment on breeding habitat (Brown et al. 2001). Evidence that humans are directly responsible for American Oystercatcher nest failure is limited (Davis et al. 2001, McGowan 2004); however, human recreation is often associated with lower oystercatcher reproductive success (Hockey 1987, Jeffery 1987, Novick 1996, Davis 1999, Leseberg et al. 2000, Verhulst et al. 2001, McGowan 2004). Because American Oystercatcher populations may require intensive management in the near future, it is important to understand the relationship between human recreation and oystercatcher nesting success (Brown et al. 2001, Davis et al. 2001).

Skutch (1949) hypothesized that higher levels of parental activity during the nesting period might lead to greater rates of predation because more activity makes nests more obvious to predators. Because American Oystercatchers are ground-nesting shorebirds that are easily flushed from their nests (Davis 1999),

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we similarly hypothesized that human recreation might increase the activity of incubating oystercatchers, thereby leading to increased predation rates. Although Skutch's hypothesis has been tested extensively, conclusions are mixed (Martin 1992, Roper and Goldstein 1987, Martin et al. 2000, Tewksbury et al. 2002). We believe that nesting American Oystercatchers provide a good opportunity to test Skutch's hypothesis because their nests are relatively easy to find and monitor, and they experience high rates of nest predation (Nol and Humphrey 1994, Davis et al. 2001, Sabine et al. 2005).

In this study, we used video monitoring to record human recreational activity and the behavior of incubating oystercatchers nesting on the Outer Banks of North Carolina. We asked whether human recreational activity altered the behavior of nesting birds, and whether increased parental activity or decreased nest attendance were associated with higher rates of nest failure.

METHODS

Study areas.—We monitored nesting success of American Oystercatchers at Cape Lookout (76° 32′ W, 34° 36′ N) and Cape Hatteras (75° 31′ W, 35° 24′ N) national seashores in North Carolina during 2002 and 2003. The seashores comprise >160 km of barrier island habitat that supports ~90 breeding pairs of American Oystercatchers. All work at Cape Lookout National Seashore was conducted on North Core Banks and South Core Banks (see Godfrey and Godfrey 1976 for site description). Cape Hatteras National Seashore comprises three main islands: Bodie, Hatteras, and Ocracoke Islands. These barrier islands are long, narrow, and bordered by sandy beaches on the ocean side and salt marshes on the sound side. American Oystercatchers nest on the ocean side beaches, dunes, and adjacent sand flats. Raccoons (*Procyon lotor*) and feral cats (*Felis catus*) are common on all islands except Ocracoke, which has no raccoons. The islands are open to the public and most beaches are open to vehicles. Approximately 650,000 people visit Cape Lookout each year; the visitation rate at Cape Hatteras is considerably higher and has increased steadily from 1.5 million in 1986 to 2.2 million in 2005 (National Park Service 2005). Park visitors use the beaches for walking, shell collecting, swimming, and fishing, and they drive four-wheel drive passenger vehicles (ORVs) and smaller, all-terrain vehicles (ATVs) on the beach. Vehicles are permitted along a network of unpaved roads behind the primary dunes and anywhere on the open beach, except in designated areas that are closed to protect vegetation, nesting sea turtles, and shorebirds, and to prevent erosion.

Data collection.—We located oystercatcher nests (n = 268) and, from 15 April until 30 July in 2002 and 2003, checked their status every 3–4 days until chicks hatched or the nests failed. We used SONY HI-8 video cameras to record the incubation behavior of nesting adults at randomly selected nests (n = 72). We videotaped nests on Bodie Island and Hatteras Island (Cape Hatteras National Seashore), and on North Core Banks and South Core Banks (Cape Lookout National Seashore). Nests were filmed for approximately 4-hr intervals at least once between the completion of egg laying and hatching. In the absence of human recreational activity, we assumed that parental behavior would be natural and homogenous throughout the incubation period. Evidence indicates that both American and Black (*Haematopus bachmani*) oystercatchers incubate their eggs 90–100% of the time once the clutch is completed, and that the amount of time spent incubating does not vary during the incubation period (Nol and Humphrey 1994, Andres and Falxa 1995). Verboven et al. (2001) showed that Eurasian Oystercatchers incubated 85–90% of the time at undisturbed nests, and that the percentage of time spent incubating was constant between the end of the laying period and hatching. Studies of other shorebird species indicate similar incubation patterns (Norton 1972), although Cartar and Montgomerie (1987) found that nest attendance of White-rumped Sandpipers (*Calidris fuscicollis*) may vary daily, depending on weather or other environmental factors.

Novick (1996) reported that human activity on South Core Banks at Cape Lookout National Seashore was distributed "fairly evenly" throughout the day and was greater on weekends (Friday–Sunday) than on weekdays. Novick (1996) also reported that humans concentrated around activity centers, such as the ferry dock, the lighthouse, and the ocean inlets at the north and south ends of South Core Banks. Our nests were filmed between 07:00 and 14:00 EST, on both weekdays and weekends, which we believe provided an unbiased representation of human disturbance and parental activity patterns at each nest.

Each video camera was housed in a weatherproof plastic container attached to a metal stand, and placed approximately 5 m from the nest to avoid disturbing incubating birds. Most cameras faced the ocean and recorded activity both in the vicinity of the nest and on open beach beyond the nest. Sometimes cameras were placed at nests located in the dunes or other locations where the ocean-side beach was not visible. In these cases, we directed cameras toward the most likely source of human recreation (e.g., the dune road at Cape Lookout). The area sampled by the video camera was different for each nest due to differences in the surrounding landscape; therefore, detection probabilities for human activities were heterogeneous among nests. We reviewed tapes in real time to count the number of trips by incubating birds to and from the nest per hr, and the percent time that adults spent incubating. Herein, the term "trip" refers to a bird leaving or returning to its nest. We also counted the number of ORVs, ATVs, and/or pedestrians passing each nest per hr.

Statistical analyses.—We used the Mayfield (1961, 1975) method to estimate daily nest survival rates and hatching success for all nests monitored. We applied the Mayfield estimate to entire clutches and did not consider individual egg survival. Heterogeneity in survival probabilities during the incubation stage was not considered, and the midpoint rule was used to designate the time of failure and time of hatching for nests that failed or hatched between visits. We considered nests successful if at least one egg hatched, and failed when all eggs were lost. Partial nest failure was not considered in this study.

Each time a bird left its nest we estimated the time between departure and the time at which the probable causal event occurred. Possible causal factors included: ATV, ORV, pedestrian, and airplane traffic, as well as interactions between territorial pairs and exchanges in incubation duties. We report these data as the percent of nest departures for which one of the above causal factors followed. We also report the percent of observed human recreational activities that were preceded by a bird leaving its nest.

We used linear regression models (Neter et al. 1996) to determine whether human recreational factors were correlated with oystercatcher parental activity. Trips per hr and percent time spent incubating were modeled as dependant variables, with number of ORVs, ATVs, and pedestrians passing a nest per hr serving as the independent variables.

For camera-monitored nests, we used the logistic exposure method to estimate daily nest survival (Shaffer 2004). We used SAS (ver. 9.1; SAS Institute, Inc. 2003) to generate survival estimates and to test competing models of nest survival with parental behaviors as covariates (Shaffer and Thompson in press). We tested 11 *a priori* models (Table 1) that modeled trip rate and percent time incubating as both continuous and categorical variables. We used two methods for categorizing the data: one purely statistical and one based on behavioral observations. For statistical categorical models, we split the data for number of trips/hr (Tripcat) and percent time incubating (Inccat) into low and high categories, using the median value of each as the cut-off point (Tripcat1: ≤ 3.69 trips/hr = low, >3.69 trips/hr = high; Inccat1: $\leq 85\%$ = low, $>85\%$ = high). For the second method (biological categorical models), we used the average values from seven nests that had no evidence of human disturbance; we then divided the data into a new set of low and high categories. In this case, undisturbed nests averaged 2.25 trips per hr. Therefore, we used three trips per hr as a conservative estimate of oystercatcher nest site activity in the absence of human disturbance (Tripcat2: ≤ 3.0 trips/hr = low, >3.0 trips/hr = high). Time spent incubating by undisturbed birds averaged 90% of the observation period; thus, we used 90% as the cut-off point to categorize nests as low or high in terms of percent time spent incubating (Inccat2: $\leq 90\%$ = low, $>90\%$ = high). We modeled each categorical variable separately and in a model that included both trip rate and percent time incubating (Table 1). One model included a year effect, and we tested a null model (null) that assumed constant survival over the season. We used an information the-

TABLE 1. Eleven candidate models used to examine the relationship between daily nest survival and parental incubation behaviors of American Oystercatchers nesting on the Outer Banks of North Carolina in 2002 and 2003.

Candidate model	Model covariates
Global Continuous	Year, trips to and from the nest per hr, percent incubation time
Year	Year
Models with statistically categorized data (splitting low and high data at the median value)	
Global categorization 1	Year, tripcat1, inccat1[a]
Tripcat1 + inccat1	Tripcat1, inccat1
Tripcat1	Tripcat1
Inccat1	Inccat1
Models with biologically categorized data (splitting data at the average value for undisturbed nests)	
Global categorization 2	Year, tripcat2, inccat2
Tripcat2 + inccat2	Tripcat2, inccat2
Tripcat2	Tripcat2
Inccat2	Inccat2
Null	No covariates, assumes constant survival

[a] Inccat1, inccat2, tripcat1, and tripcat2 are categorical variables into which nests were categorized as low or high in terms of percent time adult birds spent incubating (inccat) or the number of trips adults made to and from the nest/hr (tripcat), according to the criteria that follow: inccat1: ≤85% = low, >85% = high; inccat2: ≤90% = low, >90% = high; tripcat1: ≤3.69 trips/hr = low, >3.69 trips/hr = high; tripcat2: ≤3.0 trips/hr = low, >3.0 trips/hr = high.

oretic approach to rank the models from most to least supported, based on Akaike's Information Criterion (AIC)—using AIC_c, ΔAIC_c, and Akaike weights (w_i); Burnham and Anderson 2002). Means are reported ±SE.

RESULTS

We monitored 185 nests at Cape Lookout and 83 nests at Cape Hatteras. The overall Mayfield estimate of daily nest survival was 0.92 ± 0.006 at Cape Lookout and 0.94 ± 0.007 at Cape Hatteras. The highest daily nest survival rates were recorded at Cape Hatteras in 2003 (0.96 ± 0.008), and the lowest were recorded at Cape Lookout in 2002 (0.90 ± 0.007); these were the only year and location comparisons that were significantly different ($Z = 4.83$, $P < 0.001$).

We filmed 72 nests for a total of 320.18 hr and a mean of 4.45 ± 1.19 hr per nest. Most nests were filmed once for ~4 hr, but some were filmed twice before they hatched or failed. We excluded one nest from the analysis where it appeared that the bird's behavior was affected by the presence of the video camera. Of the 72 nests filmed, chicks successfully hatched from 19 and 53 nests failed. Sixty two percent of nest failures were due to mammalian predation ($n = 32$), 28.5% failed for unknown reasons ($n = 15$), and 11% were lost to weather, human destruction, or abandonment ($n = 6$).

Though not true experimental controls, there were seven nests at which we observed no human disturbance during filming. Birds at those nests incubated for 90% ± 0.033 of the filming period and made 2.25 ± 0.60 trips/hr compared to 82% ± 0.017 incubation and 3.66 ± 0.17 trips/hr at all other nests. The number of trips/hr at undisturbed nests was significantly lower ($t = 2.27$, $P = 0.026$) than at all other nests. The percent of time spent incubating at undisturbed nests was not significantly greater ($t = 1.34$, $P = 0.19$) than it was at disturbed nests.

We recorded 539 instances in which incubating birds departed their nests. Of those instances, ATVs were filmed within 3 min of nest departure on 136 occasions (25%) and ORVs were filmed 92 times (17%) within 3 min of departure. We recorded a total of 284 ATVs, 62% ($n = 177$) of which passed by a nest within <3 min of a bird departing its nest. We observed 1,466 ORVs pass by filmed nests, but only 11% ($n = 168$) passed by within 3 min of a bird leaving its nest. Groups or individual pedestrians were filmed 19 times (4%) within 10 min of nest departures. Of all the 110 pedestrians that we observed, 33% ($n = 36$) passed by within 10 min of a bird de-

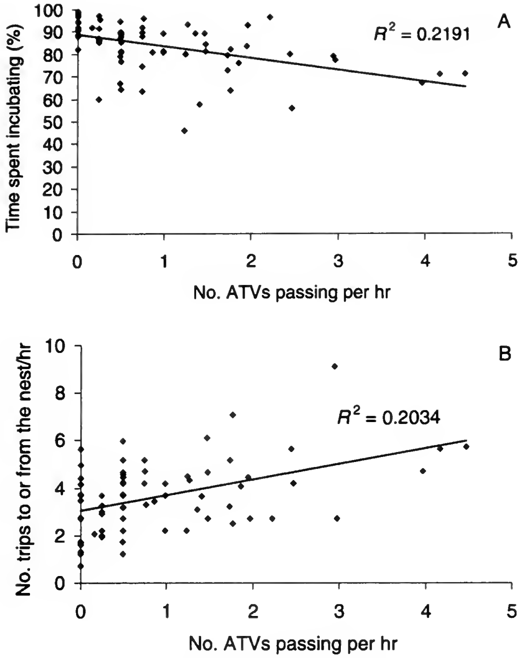

FIG. 1. The effect of all-terrain vehicle (ATV) beach traffic on incubation behavior of American Oystercatchers on the Outer Banks of North Carolina during the 2002 and 2003 breeding seasons: (A) relationship between the percent of time spent incubating and the average number of ATVs passing per hour ($\beta_1 = -0.037$, $P = 0.025$), and (B) relationship between the number of trips to and from the nest per hr and the number of ATVs passing per hr ($\beta_1 = 0.749$, $P < 0.001$).

parting its nest. Eight percent ($n = 44$) of nest departures were associated with territorial disputes and 18% ($n = 108$) with the exchange in incubation duties. Eight departures (1%) were associated with low-flying airplanes that passed within 3 min of nest departure. For the remaining 29% ($n = 154$) of nest departures, no disturbances, territorial interactions, or incubation exchanges took place following departure.

Regression models showed that there was little or no association between ORV traffic and the rate at which incubating oystercatchers made trips to and from their nests ($\beta_1 = 0.018$, $P = 0.064$) or the percent time they spent incubating ($\beta_1 = 0.0006$, $P = 0.57$). Likewise, pedestrian traffic was not associated with a significant reduction in the percent time incubating ($\beta_1 = -0.005$, $P = 0.75$) or birds making more trips to and from their nests per hr ($\beta_1 = -0.268$, $P = 0.079$). Increased ATV traffic, however, was associated with a reduction in the percent time spent incubating ($\beta_1 = -0.037$, $P = 0.025$) and an increase in the rate of trips to and from the nest ($\beta_1 = 0.749$, $P < 0.001$; Fig. 1).

All models except the global continuous model received some level of support, but no model had overwhelming support (Table 2). The tripcat2 model (i.e., nests divided into low and high categories based on average trip rate for nests with no observed human distur-

TABLE 2. Candidate models examining the relationship between daily nest survival and parental incubation behaviors of American Oystercatchers nesting on the Outer Banks of North Carolina in 2002 and 2003. Models are ranked in descending order of support based on Akaike's information criteria AIC_c, ΔAIC_c, and Akaike weights (w_i).

Model	Log-likelihood	No. parameters	AIC_c	ΔAIC_c	w_i
Tripcat2[a]	−159.62	2	323.27	0.00	0.28
Null	−161.08	1	324.16	0.89	0.18
Tripcat2 + inccat2[a]	−159.62	3	325.29	2.02	0.10
Inccat1	−160.68	2	325.39	2.11	0.097
Inccat2	−160.77	2	325.56	2.29	0.089
Tripcat1	−160.98	2	325.99	2.72	0.072
Year	−161.07	2	326.17	2.90	0.066
Tripcat1 + inccat1	−160.26	3	326.56	3.29	0.054
Global categorical2	−159.56	4	327.18	3.92	0.040
Global categorical1	−160.24	4	328.54	5.28	0.020
Global continuous	−261.36	4	530.79	207.52	0.000

[a] Inccat1, inccat2, tripcat1, and tripcat2 are categorical variables into which nests were categorized as low or high in terms of percent time adult birds spent incubating (inccat) or the number of trips adults made to and from the nest/hr (tripcat), according to the criteria that follow: inccat1: ≤85% = low, >85% = high; inccat2: ≤90% = low, >90% = high; tripcat1: ≤3.69 trips/hr = low, >3.69 trips/hr = high; tripcat2: ≤3.0 trips/hr = low, >3.0 trips/hr = high.

TABLE 3. Daily survival estimates and hatching probability estimates for nests in two categories of behavioral data collected from American Oystercatchers nesting on the Outer Banks of North Carolina in 2002 and 2003.

Category	No. nests	Daily probability of survival	Lower / upper confidence intervals	Hatching probability
Median cutoffs				
≤3.69 trips/hr	37	0.958	0.935 / 0.973	0.314
>3.69 trips/hr	35	0.948	0.925 / 0.965	0.240
Incubation ≤85%	32	0.961	0.938 / 0.975	0.338
Incubation >85%	40	0.945	0.922 / 0.962	0.218
Zero-observed-disturbance average cutoffs				
<3.00 trips/hr	26	0.969	0.946 / 0.982	0.424
>3.00 trips/hr	46	0.944	0.924 / 0.960	0.213
Incubation <90%	50	0.967	0.945 / 0.980	0.400
Incubation >90%	22	0.948	0.926 / 0.964	0.237

bance as the only covariate) had the highest rank of all the models ($\Delta AIC_c = 0.00$, $w_i = 0.28$). The null model was ranked second ($\Delta AIC_c = 0.89$, $w_i = 0.18$), and the model incorporating both tripcat2 and inccat2 was ranked third ($\Delta AIC_c = 2.02$, $w_i = 0.10$). All the models with categorical behavioral variables, the year model, and the null model had a ΔAIC_c of <7 and weights between 0.02 and 0.28 (Table 2). Generally, models with a ΔAIC_c of <7 cannot be ruled out, but models with weights <0.70 cannot be exclusively accepted (Burnham and Anderson 2002).

The estimated daily survival rate for nests with ≤3.69 trips to and from the nest per hr was greater than the daily survival rate for nests with >3.69 trips to and from the nest per hr (Table 3). That same pattern was observed when the data were divided into categories representing nests with ≤3 trips per hr and >3 trips per hr. Nests in which the parents incubated for ≤85% of the observation period had higher daily survival probabilities than nests in which incubation percentages were >85%. The same pattern was observed when we categorized the data by nests in which adults spent ≤90% and >90% time incubating. These data indicated that nests in which parents made more trips to and from the nest had a lower daily survival probability, and that nests where the parents spent more than 85–90% of their time incubating had a lower chance of surviving each day.

DISCUSSION

Our data show clear associations between human recreation and incubation behavior of American Oystercatchers. ATV traffic was associated with increased rates of trips to and from the nest and reduced time incubating; other forms of human recreation were more weakly associated with oystercatcher nesting behaviors. Sixty two percent of the ATVs that we observed passed within 3 min of a bird departing its nest, whereas the same was true for only 11% of the ORVs that we observed. Birds appear to have habituated to the presence of ORVs (Whittaker and Knight 1998), but they view ATVs (and to a lesser extent, pedestrians) as threats. Peters and Otis (2005) reported that wintering American Oystercatchers habituated to boat traffic on the intercoastal waterway in South Carolina. Other studies have shown that birds respond differently to different forms of human recreational disturbance (Burger 1981), but most have focused only on changes in foraging behavior (Burger and Gochfeld 1998, Rodgers and Schwikert 2003, Stolen 2003). Our study is one of the few to investigate how human recreational disturbance affects incubation behavior. ATVs are louder and move faster than ORVs and pedestrians, which might explain why the birds are affected more by ATV traffic (Burger 1981, Burger and Gochfeld 1998). ORVs and pedestrians also tend to stay closer to the firm sand along the water's edge, which means they generally travel farther from nesting birds.

Although the probability of hatching was low in all nests, regardless of parental activity, we did find evidence that human recreational disturbance may reduce the nesting success of

American Oystercatchers by altering incubation behavior. Analyses based on AIC model selection indicated that the rate of parental trips to and from the nest and the percent time that parents spent incubating may have affected daily nest survival rates. Although no model received overwhelming support, none of the categorical behavioral models could be ruled out. The daily survival estimates indicated that nesting adults that made fewer trips to and from the nest had greater daily nest survival rates. Conversely, nests where the parents incubated for less time had higher daily survival rates. We hypothesize that mammalian nest predators, the primary nest predators in this system (Davis et al. 2001), are better able to find disturbed nests through smell because each time a parent gets up and walks away from a nest it leaves a scent trail that raccoons and cats may follow. Our results differ from those of Verboven et al. (2001), but that is likely because the primary nest predators in that system were avian predators.

ATV traffic is not the only factor affecting oystercatcher nesting success on North Carolina's Outer Banks. Nest predation is an important determinant of hatching success in the Outer Banks (Davis et al. 2001, McGowan et al. 2005), and relationships between human recreation and nest predators are poorly understood. Vehicular traffic also may affect success during the chick-rearing phase of reproduction. In the 2003 breeding season, we confirmed that five chicks from three different nests were run over by vehicles on the beaches of South Core Banks at Cape Lookout National Seashore and Hatteras Island at Cape Hatteras National Seashore (McGowan 2004).

The negative association between percent time incubating and daily nest survival seems counterintuitive. Conway and Martin (2000) showed that birds balance the costs of egg exposure with those of high parental activity. Birds with high levels of nest-predation pressure minimize nest-site activity by taking fewer, longer trips off the nest (Conway and Martin 2000). This behavior helps reduce parental activity around the nest, but it also reduces the amount of incubation. American Oystercatcher behavior may reflect a similar trade off; their eggs can tolerate extensive heating and cooling (Nol and Humphrey 1994). In our study, several clutches exposed for approximately 1 hr at mid day hatched successfully. One videotaped nest hatched successfully, even though the parents incubated for only 66.8% of the 4.07-hr observation period. Egg hardiness may reflect an adaptation that enables parents to reduce nest-site activity. Parents that depart their nest and wait until multiple disturbances have passed before returning may have greater nesting success than parents that return to their nests quickly and flush repeatedly. Future analyses should assess the effect that the average amount of time birds spend off the nest has on nest success.

There were several potential sources of measurement error in our study that might explain why no models were strongly supported. Incubation behavior might vary as birds habituate to disturbance (Whittacker and Knight 1998). Because the field of view varied at each nest, our cameras recorded areas of different size for each nest, and we were unable to control for these differences in the analyses. We were also unable to measure the distance from the nests to the disturbance recorded on our video. Several studies have shown that the proximity of human disturbance has a major effect on the behavioral responses of birds (Burger and Gochfeld 1998, Rodgers and Schwikert 2003). It is likely that in some cases, recreational activity recorded by our cameras did not elicit a response from the incubating bird because the activity was too far away. Video monitoring is an extremely useful tool for studying avian behavior; however, future studies of human disturbance using video monitoring should entail measuring distances to sources of disturbance. Recording nests for longer periods of time also would alleviate a great deal of uncertainty. Sabine et al. (2005) were very successful in studying nest success of oystercatchers in Georgia by using time-lapse videography throughout the incubation period.

Our simplified approach of categorizing nests into low or high levels of parental activity provided a coarse-scale observational measure of behavioral responses to recreation and disturbance; we expected this to reduce observation errors. Other researchers that have evaluated the effects of human disturbance on avian behavior used experimental designs with defined treatment groups (Robert and Ralph 1975, Tremblay and Ellison 1979, Verhulst et al. 2001, Stolen 2003). We studied the effects of ambient human disturbance caused by park staff and recreational visitors to determine whether it was linked to patterns of nesting success. Future studies of human activity and oystercatcher nesting success that compare the behavior of birds on beaches closed to vehicle and pedestrian traffic with the behavior of birds exposed to different types and intensities of human activity are needed to improve our understanding of the patterns suggested by this study.

ACKNOWLEDGMENTS

We are grateful to J. R. Cordes and M. Lyons for their tremendous contributions to this study. We thank the National Park Service, the U.S. Fish and Wildlife Service, and the U.S. Geological Survey for supporting this research. We thank M. W. Rikard and the staff of Cape Lookout National Seashore, and S. Harrison and the staff at Cape Hatteras National Seashore, for all their assistance. We thank J. A. Collazo, K. H. Pollock, and F. R. Thompson, III, for assistance on the design and analysis of this study, and J. Hostetler and M. S. Pruett for their assistance with data collection and management. We thank C. C. McGowan for editing this manuscript. We are grateful to three anonymous reviewers for their comments and suggestions for improving this manuscript.

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The Wilson Journal of Ornithology 118(4):494–501, 2006

MOVEMENTS OF LONG-TAILED DUCKS WINTERING ON LAKE ONTARIO TO BREEDING AREAS IN NUNAVUT, CANADA

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ABSTRACT.—We used implanted satellite transmitters to track the northbound (spring) and southbound (fall) migration and possible breeding locations of three Long-tailed Ducks (*Clangula hyemalis*) wintering on western Lake Ontario in Ontario, Canada. The birds exhibited short, rapid migration movements punctuated by extended periods of up to 30 days at staging areas. For much of the nesting period (~10 June to 10 July), the birds remained inland of western Hudson Bay in Nunavut. During fall migration, they circumnavigated Hudson Bay to its eastern coast, opposite the coast they had followed in spring, for a mean travel distance of 6,760 km. Identification of these previously unknown, key migration sites fills some important information gaps on Long-tailed Ducks in eastern Canada, and it augments what is known about important coastal marine habitats in the Arctic. *Received 28 June 2005, accepted 24 March 2006.*

The Long-tailed Duck (*Clangula hyemalis*; formerly Oldsquaw) is a medium-sized sea duck with a circumpolar distribution, found across North America (Robertson and Savard 2002). It is purportedly the most numerous species of sea duck, although population estimates are unreliable (Bellrose 1980, Robertson and Savard 2002). North American populations winter principally along the Pacific (45° to 60° N) and Atlantic (35° to 53° N) coasts, where declines in abundance have been reported (Robertson and Savard 2002); some Long-tailed Ducks overwinter on the Great Lakes. Despite the species' ubiquitous presence along coasts and on large lakes in winter, and its widespread breeding distribution, we know little of the biology and movements of this species other than what was reported by Alison (1975) and Peterson and Ellarson (1979). This is likely attributable to three factors: (1) the species is not harvested heavily, so there has been little historical pressure to gather information about it; (2) it breeds in low densities and is dispersed across remote tundra (e.g., Pattie 1990), which makes banding studies difficult to initiate; and (3) its breeding range lies outside the areas covered by annual North American waterfowl surveys (Cowardin and Blohm 1992). However, recent concern about population declines among many sea duck species has prompted scientific investigation of the Long-tailed Duck (Sea Duck Joint Venture Management Board 2001).

A significant information need for the Long-tailed Duck is the delineation of areas used by different populations and the bird's movements between breeding, molting, and wintering areas. Prior observations during southbound (fall) migration suggested that Long-tailed Ducks in Hudson and James bays move south, probably along river systems, to the Great Lakes (Bellrose 1980, Leafloor et al. 1996, Robertson and Savard 2002). More recently, technological advances have allowed biologists to track birds remotely, thus providing new insights into the movements and ecology of many species (e.g., Brodeur et al. 2002, Robert et al. 2002, Petrie and Wilcox 2003). We use data gathered from Long-tailed Ducks implanted with satellite transmitters to describe their movements (1) from their capture in late winter on the Canadian Great Lakes to breeding areas and (2) during fall migration from the eastern Canadian Arctic. We predicted that Long-tailed Ducks would move north from the Great Lakes to James Bay, nest along Hudson Bay, and then return along the same route in fall migration.

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METHODS

We captured Long-tailed Ducks on 27 March 2003 and 30 March 2004 at the mouth of the Niagara River near the town of Niagara-On-The-Lake (43° 15′ N, 79° 4′ W). To capture the birds, we used mist nets suspended across observed feeding areas, similar to procedures described by Brodeur et al. (2002) for capturing Harlequin Ducks (*Histrionicus histrionicus*). Captures took place in the morning (~06:00 EDT) when light was still low and birds probably had difficulty seeing the mist net. Captured birds were placed in dark containers and moved to a nearby, temporary surgical suite. We implanted transmitters into nine ducks, although only three provided us with migration data. We believe that the transmitter antenna on one bird moved or was impaired, as we received sporadic transmissions without location information for 2 months after surgery. The other five ducks stopped transmitting within 2 weeks of surgery, probably due to mortality.

Satellite transmitters were supplied by Microwave Telemetry, Inc. (Columbia, Maryland; Model PTT-100 Implantable), and weighed approximately 39 g. As such, the target weight for birds into which these transmitters would be implanted was 780 g (i.e., transmitters were 5% of their body mass). However, we experienced considerable difficulty, both in capturing birds and in finding birds of this size. At the time of implantation, the three birds that we tracked weighed 779 g (male), 740 g (female), and 700 g (male); thus, the transmitters represented 5.0, 5.3 and 5.6% of their body mass, respectively. Captured birds (2 males, 1 female) were held in captivity for 302 ± 80 (SD) min, which included 71 ± 5 min of anesthetization and 33 ± 9 min of surgery. Each transmitter was surgically inserted in the right abdominal air sac of the anesthetized duck, and each had a transcutaneous antenna that exited cranially to the synsacrum. Surgical and anesthetic procedures followed those described by Fitzgerald et al. (2001). Birds were released at the capture site after the effects of anesthesia wore off.

Radio-marked birds were tracked using the ARGOS satellite system. Transmitters were duty-cycled on a schedule of 8 hr on followed by 72 hr off (for 24 cycles); subsequently (for the remainder of their battery life, approximately 60 cycles), their schedule shifted to 8 hr on followed by 48 hr off. Because our sample size was small, we used data with ARGOS codes 0–3 (accuracy <1,000 m); however, we also included some Auxiliary Processing locations (ARGOS codes A, B, C, and Z; no estimate of accuracy; ARGOS 1996), despite the reduced confidence in their accuracy. To determine whether to include a given location coded as A–C or Z, we compared it to locations documented before and after the record in question; if it was along the same flight path or within a few km of areas where the birds were staging, the location was retained. Outlier data were generally obvious—well off the flight path and/or indicating distances not achievable from the high-accuracy locations. On days when we received only data with low accuracy codes, data were excluded. This project was carried out according to protocols approved by the Canadian Council on Animal Care. All means are reported ±SD.

RESULTS

Transmitter performance.—We received 1,747 transmissions from the three implanted birds, of which 1,203 (69%) provided usable information on locations. One duck provided 67% of the data, but this was attributed to more frequent transmissions per day, not a longer transmission period. The three transmitters provided a mean performance of 582 transmissions and 401 locations over 217 days and 6,760 km of travel.

Bird movements.—The two male Long-tailed Ducks spent most of April 2003 on Lake Ontario near the capture site; on 27–28 April, they moved to Georgian Bay on Lake Huron (45° 29′ N, 80° 40′ W), where they staged for the next 23 and 30 days, respectively (Figs. 1, 2A). This was followed by a rapid migration to northwestern James Bay (54° N, 82° W); transmissions were 3 days apart, and one bird had arrived at this site from Lake Huron between consecutive transmissions. The males stayed in northwestern James Bay for approximately 2 weeks (Fig. 2B), and then moved to western Hudson Bay (58° 3′ N, 93° 14′ W and 63° 53′ N, 95° 31′ W) for the last 3 weeks of June and the 1st week of July (Fig. 2C); during that time, they moved only very short distances from inland

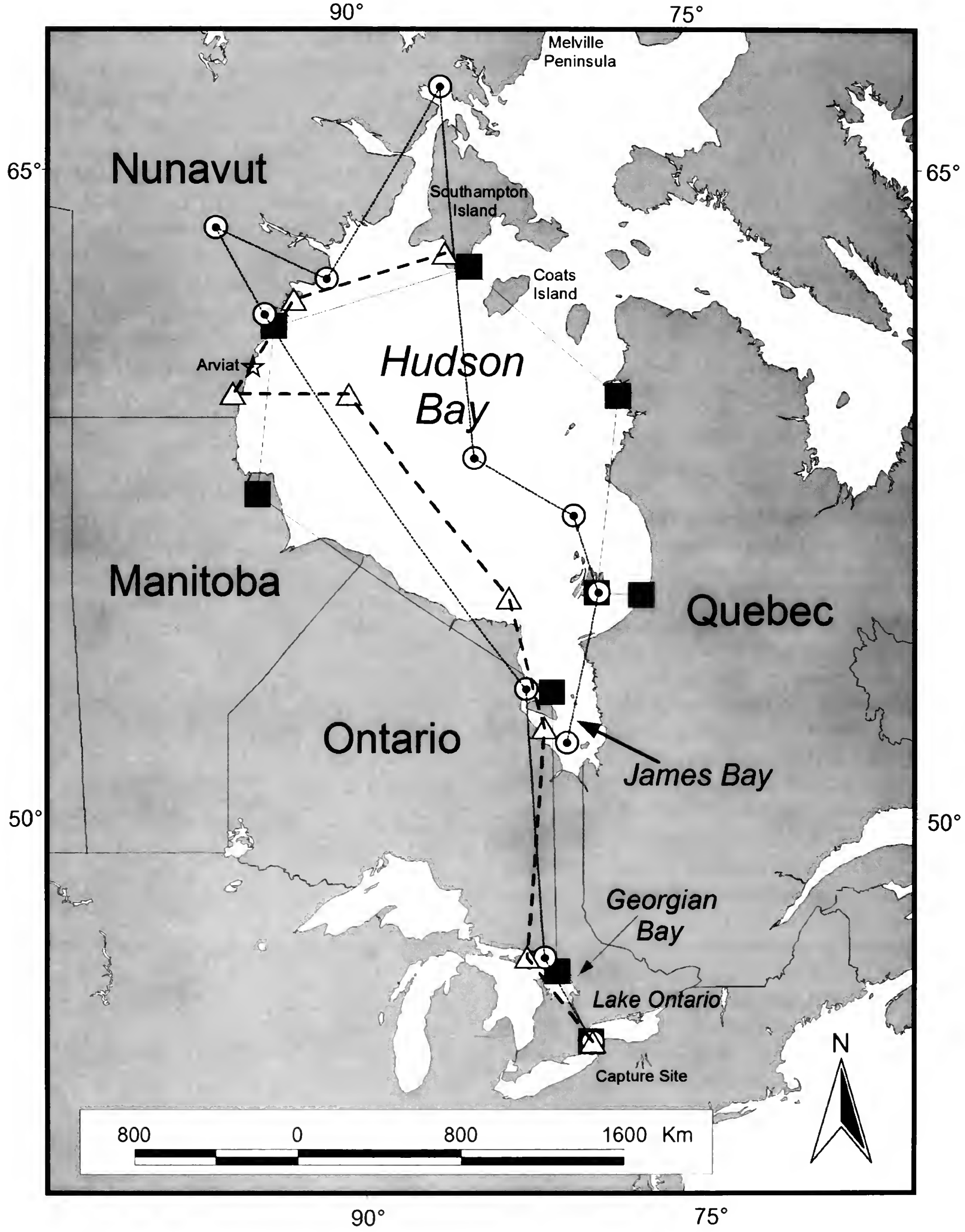

FIG. 1. Movements of two male and one female Long-tailed Duck captured at Niagara-On-The-Lake, Ontario, Canada, in 2003 (males: squares and circles) and 2004 (female: triangles). Lines represent tracked or interpolated flight paths.

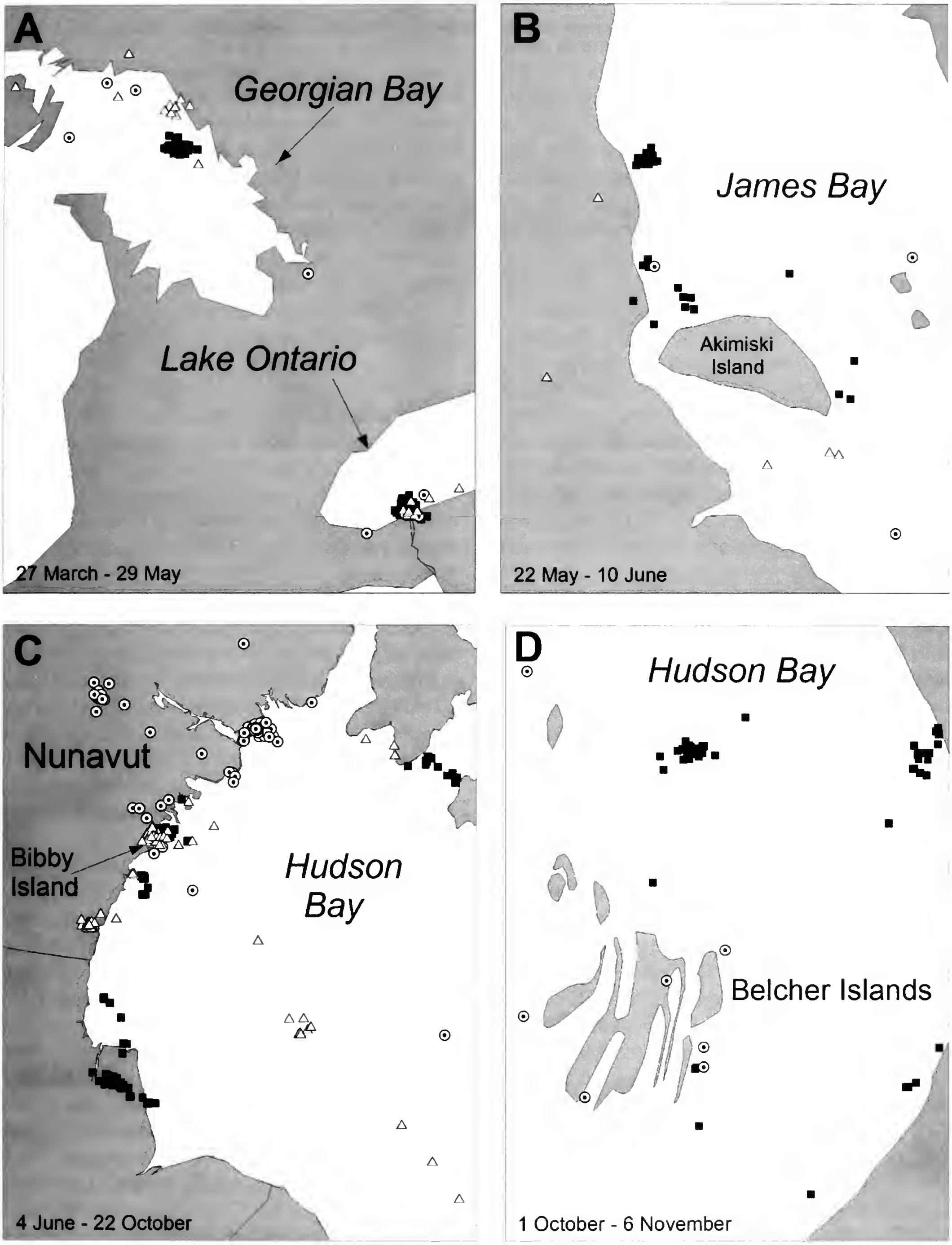

FIG. 2. Details of staging and apparent breeding locations used by Long-tailed Ducks that moved from Ontario to Nunavut, Canada, in 2003 (males: squares and circles) and 2004 (female: triangles).

locations and we assumed that each was attending a mate at a nest site. For much of the summer (12 July to 18 September, and 10 July to 31 August), the males moved to a coastal location near Bibby Island (61° 56′ N, 93° 14′ W). One male departed this site in early September and moved farther north to southern Melville Peninsula (66° 23′ N, 85° 46′ W), where he stayed from 10 to 18 September. The other male moved to southern Southampton Island (62° 53′ N, 83° 36′ W), where he stayed from 24 to 28 September; by 1 October, this male had migrated east across Hudson Bay and remained near the Belcher Islands (Fig. 2D; 56° 30′ N, 79° 30′ W) and eastern Hudson Bay until transmissions ceased on 6 November. The second male remained farther north, but by 20 October, he had migrated southward to Coats Island (62° 30′ N, 82° 30′ W); by 6 November, he had moved farther south to eastern James Bay, where his radiotransmitter failed (also on 6 November).

In 2004, the female exhibited a movement pattern similar to that of the males in 2003 (Fig. 1). The duck remained in western Lake Ontario until 27 April; by 3 May, she had moved to Georgian Bay, Lake Huron, where she remained until 31 May. By 2 June, the bird had migrated north to western James Bay, where she stayed until 29 June. Unlike the males, this female then spent from 30 June to 10 July moving northwest across Hudson Bay, well offshore, before heading inland in Nunavut south of Arviat (61° 28′ N, 93° 48′ W). The female remained inland until 4 August, and then moved slightly north and offshore to the coast around Bibby Island, where she remained until 17 October. By 20 October, the bird had moved north to the southwestern coast of Southampton Island (63° 30′ N, 86° 38′ W), where she remained until at least 31 October, at which time her radiotransmitter failed. During the two monitoring periods (April to October, 2003 and 2004), the three radio-marked birds spent 12% of their time at Georgian Bay, 7% at James Bay, and 30% near Bibby Island, western Hudson Bay.

Flight speeds.—Flight (ground) speeds of the three Long-tailed Ducks were calculated for several days when their transmissions indicated continuous movement (i.e., locations traced a linear track). The birds traveled at 50.2 ± 16.8 km/hr ($n = 5$ days). On 22 October 2003, however, one male's transmitter recorded a southward movement that started at 08:35, when the bird was positioned at 59° 6′ N, 84° 18′ W. By the time the transmission period ended at 15:30, the bird had moved south to 55° 54′ N, 78° 48′ W, which represents a straight-line distance of ~600 km in 7 hr, or a flight speed of 86 km/hr. Unfortunately, the duty cycle on the transmitters did not allow us to reliably assess whether birds were more likely to move at day or night. All of the movements used to calculate flight speeds were recorded between 00:40 and 16:30.

DISCUSSION

The data gathered in this study provide new insights into the habitat use and migration patterns of Long-tailed Ducks in eastern North America. Radio-marked Long-tailed Ducks wintering on western Lake Ontario moved northwest to breed along western Hudson Bay, and then appeared to circumnavigate Hudson Bay before traveling southward along its eastern coast during fall migration. The latter finding was unexpected and counter to our predictions, as there was no previous evidence of this circuitous movement pattern. Our interpretation assumes that the implantation procedure did not markedly alter the birds' travel routes and migration patterns. We believe this to be a reasonable assumption because the findings of prior studies have suggested similar migratory patterns linking these regions (Bellrose 1980, Leafloor et al. 1996). The information provided by the satellite transmitters confirms this pattern, and we identified some key staging locations. Despite our small sample size, the similarity of movements in both years and by both sexes attests to the importance of the key sites.

Long-tailed Duck migration northward from the Great Lakes takes place in a series of short, rapid movements, separated by relatively long stopovers at certain major coastal sites. Northern Georgian Bay in Lake Huron (Fig. 2A) and western James Bay, particularly north of Akimiski Island (Fig. 2B), appear to be critical stopover sites for this species during spring migration, as birds spent nearly 20% of their time between April and October in these bays. The importance of James Bay to migrating waterfowl has been known for some time and led to creation of the James

Bay Preserve in the early 1900s (reviewed in Mallory and Fontaine 2004). Our data provide further evidence of the importance of the northwestern coast of James Bay to certain sea ducks (Mallory and Fontaine 2004).

Both male and female Long-tailed Ducks wintering on western Lake Ontario migrated north and apparently bred inland along western Hudson Bay. We believe that the males attended their mates for a period of about 4 weeks before moving to molting sites some time between 10 and 12 July. This interpretation of the satellite data is consistent with Alison's (1975) observations that males left their breeding ponds near Churchill, Manitoba, on about 10 July. In 2004, the implanted female staged near Akimiski Island much longer than the males had in 2003, perhaps due to the winter conditions that persisted relatively late along western Hudson Bay that year. When the female finally moved to the breeding area, she stayed well offshore and flew over sea-ice (Environment Canada 2005), counter to the expected pattern of following shorelines (Johnson 1985). The female was positioned inland at potential nesting areas for a period of 25 days beginning around 10 July. If she nested, her nest would have been initiated about 1 month later than those of most Long-tailed Ducks nesting in that region (Alison 1975); thus, if she did nest, we suspect that her nest was abandoned or depredated. Female Long-tailed Ducks require ~33 days to lay and hatch an average-sized clutch (7 days for laying plus 26 days for incubation), longer than the amount of time the radiomarked duck spent in that area. It is also possible that implantation of the transmitter into her celomic cavity could have affected oviposition and normal nesting behavior, or it is possible that she had not yet reached breeding age (which also could have explained some of her erratic movements).

An important finding of our study was the location of a molting area near Bibby Island, between Arviat and Whale Cove, Nunavut, where the three ducks spent 30% of their time during the study period. This site was previously unknown, and demonstrates the utility of satellite transmitters for revealing important, but remote and undiscovered, sites used by some migratory bird species (e.g., Brodeur et al. 2002). The male Long-tailed Ducks moved to the area around Bibby Island after leaving their breeding ponds, whereas the female arrived somewhat later; both the male and female arrival dates were similar to those reported for their respective sexes at molting sites elsewhere (Johnson and Richardson 1982, Johnson 1985). All three birds spent up to 2 months in the shallow waters around the coast near Bibby Island. The proportion of the overall Long-tailed Duck population that molts at this site, and the extent to which this area supports molting birds of other waterfowl species, should be investigated.

There was considerably more variation in the pattern of fall migration among the three birds. The males moved east from molting sites, then south along eastern Hudson Bay. One male spent a month near the Belcher Islands; the other male followed the same general pathway, but did not arrive in eastern Hudson Bay until 3 weeks after the first male. Given that many Long-tailed Ducks overwinter in polynyas near the Belcher Islands and in western Hudson Bay (Robertson and Savard 2002), birds in our study may not have continued southward. The female appeared to be following the same path as the males, but initiated her fall migration relatively late and had only moved to Southampton Island by the time her radiotransmitter failed in late October. During fall migration, Leafloor et al. (1996) collected birds in northern Ontario; given that the birds had fat stores sufficient for migration, they postulated that offshore sites in Hudson and James bays must be important to Long-tailed Ducks for gathering nutrients. Our data support their hypothesis. Given the varied locations where our radiomarked birds spent their post-molting period, it appears that there may be many locations where the birds can gather food, unlike the more limited number of locations suggested by our spring migration data.

The transmitters provided performance similar to that observed for swans (Petrie and Wilcox 2003), with almost 70% of the data being usable. The flight speeds we calculated were similar to values reported previously for Long-tailed Ducks (up to 90 km/hr; Bergman 1974), but a better assessment would be possible with a duty cycle setting on the transmitters that would provide more transmissions during movement periods. The ducks in our study were at the lower body-size limit recommended for the satellite transmitters available to us at the time (e.g., Caccamise and Hedin 2003), and some of our birds were smaller than we would have preferred (i.e., transmitter weight >5% of body mass). The newer, smaller transmitters (http://www.microwavetelemetry.com) available today should allow researchers to better track smaller birds.

The data gathered by tracking the three Long-tailed Ducks in our study has provided valuable new information on the species' movements and habitat use; however, the utility of these data are not restricted to this species. For example, in a study of Peregrine Falcons (*Falco peregrinus*) breeding along western Hudson Bay, Johnstone et al. (1996) noted that the falcons there contained higher contaminant loads than birds elsewhere in the Canadian Arctic. They speculated that falcons were accumulating these contaminants from migratory prey, notably Black Guillemots (*Cepphus grylle*; marine piscivores; Mallory et al. 2005) and Long-tailed Ducks, which presumably have been accumulating pollutants from the heavily contaminated Great Lakes. Our data on movements of Long-tailed Ducks support this linkage to the Great Lakes and raise concerns that Long-tailed Ducks may transport contaminants to Arctic ecosystems.

ACKNOWLEDGMENTS

We are grateful to the many people who assisted with various aspects of this project, and the Niagara-On-The-Lake Sailing Club. Two anonymous referees and G. J. Robertson provided helpful, critical reviews of the manuscript. Financial support was provided by Environment Canada (CWS–OR and PNR), and the Sea Duck Joint Venture. This research was conducted under permits CA 0118 and 2003PNR015.

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The Wilson Journal of Ornithology 118(4):502–507, 2006

FEMALE TREE SWALLOW HOME-RANGE MOVEMENTS DURING THEIR FERTILE PERIOD AS REVEALED BY RADIO-TRACKING

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ABSTRACT.—Tree Swallows (*Tachycineta bicolor*) show one of the highest levels of extra-pair mating among bird species, yet extra-pair copulations are rarely observed. Despite the suggestion that extra-pair copulations could be taking place away from nest sites, very little is known about movement patterns of individual Tree Swallows during the pre-laying and laying periods. We used radio telemetry to track movement patterns of four female Tree Swallows at dawn and dusk during the pre-laying and laying periods. Our tracking results indicate that individual females differed in their movement patterns: some remained close to their nest site on multiple nights while others were rarely detected near their nest box at night. Despite differences in movement patterns, all four females that we tracked produced extra-pair offspring for which we were unable to identify extra-pair sires, even after sampling the majority of males breeding within our nest-box grids. Despite the small sample size, our results confirmed extensive Tree Swallow movement away from nest-box grids during the pre-laying and laying periods. This highlights the need for future studies of mating behavior away from the nesting site, particularly for species that forage and/or roost in communal areas during their fertile period. *Received 25 July 2005, accepted 17 April 2006.*

While genetic evidence of extra-pair fertilizations among birds is widespread, less is known about the behaviors that lead to extra-pair copulations (EPCs; Westneat and Stewart 2003). In the Tree Swallow (*Tachycineta bicolor*), within-pair copulations take place extremely frequently and are clearly visible. EPCs, however, are rarely observed (Venier and Robertson 1991, Lifjeld et al. 1993, Venier et al. 1993), despite the high levels of extra-pair paternity (up to 80% of all females in a population produce extra-pair young; Barber et al. 1996). Indeed, extra-pair copulations can be difficult to observe, and many researchers have used radio telemetry for following both male and female birds during their extra-territorial forays in an attempt to document extra-pair mating behavior (Smiseth and Amundsen 1995, Neudorf et al. 1997, Pitcher and Stutchbury 2000, Mays and Ritchison 2004).

Although many passerines defend all-purpose territories for foraging and nesting (but see Reyer et al. 1997), Tree Swallows defend only the area immediately surrounding their nest site (e.g., the nest box). Often they leave their territory for long periods of time, presumably to forage and roost (Hayes and Cohen 1987, Robertson et al. 1992; MKS pers. obs.). During these off-territory forays, Tree Swallows often are found in groups comprising many potential copulation partners (Robertson et al. 1992, Dunn and Whittingham 2005). Dunn and Whittingham (2005) found that, on subsequent nights, female Tree Swallows used different roost sites often comprising hundreds of individuals. Hayes and Cohen (1987), however, radio-tracked several breeding male Tree Swallows at dusk and reported that they "tended to return to the same grove night after night."

Examining potential intra-specific variation in behavioral patterns can be valuable for understanding the underlying forces that shape a species' mating system (see Westneat and Stewart 2003). In this study, we used radio telemetry to track female movements in an Ontario population of Tree Swallows. Specifically, we recorded first- (dawn) and last- (dusk) known locations of individual Tree Swallows each day during the pre-laying and laying periods. For each female, we determined her relative roosting location (i.e., on or off the nest-box grid) and the maximum distance from her nest box she was detected each day. In addition, we conducted parentage analysis on the offspring of all four focal females, evaluating extra-pair fertilizations in light of their movement and roosting patterns.

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METHODS

Our study, conducted during the 2002 breeding season at Queen's University Biological Station in Chaffey's Locks, Ontario, Canada (44° 34′ N, 76° 20′ W), focused on the area surrounding eight grids of nest boxes (6–39 boxes per grid, 0.28–1.92 ha; see Kempenaers et al. [1998] for details regarding nest-box arrangement). During the early part of the breeding season, Tree Swallows in our population generally spent the morning hours defending their nest sites as well as building nests. During the late afternoon and evening hours, however, often they were absent from the nesting grid, presumably to forage in areas with higher concentrations of insects. Despite high levels of extra-pair paternity, male Tree Swallows do not guard their mates (Leffelaar and Robertson 1984), and there is evidence that females are able to select and reject copulation partners, at least in the area immediately surrounding the nest site (Lifjeld and Robertson 1992).

Telemetry.—Four female Tree Swallows were radio-tracked during the pre-laying and laying periods. To each female, we attached an LB-2 radio transmitter (0.52 g; Holohil Systems Ltd., Carp, Ontario), secured with a figure-eight style leg harness (Rappole and Tipton 1991). To track radio-tagged birds, we used R-1000 receivers (Communications Specialists, Inc., Orange, California), 3-element and 5-element hand-held Yagi antennae, and an omni-directional antenna. We used two methods of tracking: opportunistic and systematic. The opportunistic method consisted of constantly monitoring all active transmitters while driving along roads, as well as hiking into areas inaccessible to vehicles surrounding the Tree Swallow grids. The other method involved systematically surveying a general area from a pair of pre-established look-out points separated by ~125–1,500 m: two observers (one at each point) equipped with a receiver, directional antenna, and a handheld two-way communication radio would simultaneously document the location of a given female. We were able to detect signals up to ~2,600 m away. In both methods, all frequencies were scanned continuously, and, when a signal was detected, observers would simultaneously record the compass bearing of the signal. When the precise angle could not be determined, a range of angles that encompassed the signal was recorded. Birds were tracked opportunistically throughout the day (04:00–22:00 EST), as well as systematically during morning (05:00–0:700) and evening (19:00–21:00) hours. At the end of an evening tracking session, observers visited each grid to confirm the presence or absence of focal birds in their nest boxes. The total radio-tracking effort was 100 hr. Radio transmitters were removed from birds during the incubation period.

Roosting areas.—We were unable to visually locate any roosting sites (except when birds roosted in their nest boxes) because consistent radio signals often were not detectable during nighttime hours (evidence that a bird had settled into a roost site). We also attributed the lack of nighttime signals to the birds roosting beyond receiver ranges (i.e., ≥2.6 km) or to signals being blocked by terrain (i.e., birds roosting low in a valley). When a signal was detected consistently after sundown, it was usually because the bird was roosting in her nest box. In the few cases where a bird was suspected of roosting outside of her box but near the grid, difficulties with navigating the hilly terrain in the dark precluded visual confirmation of the roosting site. Thus, we focused our efforts on estimating the general location of each bird through triangulation early in the morning (05:00–07:00) and at dusk (19:00–21:00). We used the first and last known locations of individuals as an indication of general roosting area. When we were unable to detect a given individual's signal during our evening observation period, we were able to determine only that the bird was not in the box (i.e., away from the nest grid).

Mapping.—Compass bearings were entered onto a GIS-based topographic map of the area, and bird locations, as determined from triangulation, were plotted using AutoCAD (Autodesk 2000). For a given individual on a given day, we defined "first-known location" as the bird's location when detected for the first time prior to 08:00; "last-known location" was the bird's location when detected for the last time after 21:00. The "farthest location" was the greatest distance between the bird's location and its nest box, regardless of time of day. If a signal was recorded as coming from a range of compass directions, the mean of the reported directions was used and the location of the bird was recorded as being at the intersection of the two vectors. If the vectors of the means did not cross, then the range was plotted for each observer and we recorded the bird's location as being at least as far as the closest point where the two ranges overlapped. If the two vectors did not overlap but came from the same direction (presumably due to a moving bird), the bird's location was plotted as being at least as far as the observer look-out points when these points were between the nest box and the bird's presumed location. Therefore, our reported bird locations are conservative estimates, reflecting the closest a bird could have been to its nest box within the range detected. Distance from the focal bird's nest box to each location detected during observation periods was calculated with AutoCAD (Autodesk 2000) as the straight-line distance between the two points.

Movement.—For each female, we defined the pre-laying period as the day the transmitter was attached until the day before the first egg was laid (i.e., day "−X" until day "−1"). The laying period included the day the first egg was laid (i.e., day "0") and continued until the day the penultimate egg was laid or the transmitter stopped working, whichever was later (i.e., day 0 until day "X"). The average maximum distance each female traveled during each period (pre-laying and laying) was calculated by summing the greatest distance recorded each day and dividing by the number of days on which the bird's location was recorded. The number of days on which we had detected a distance varied between females due to differences in how long the pre-laying period lasted and/or failure to detect a bird on a particular day.

Paternity.—We used 11 hypervariable microsatellite loci (total probability of exclusion = 0.999) to determine parentage of eggs and nestlings produced by the four focal females. To assign paternity to extra-pair offspring, we genotyped all males caught in surrounding nest boxes (n = 78 males). We also used genotypic data collected from males for a separate study in 1997, 2000, 2001, and 2003 (n = 65), because some of those males may have been present, but not caught (e.g., breeding in natural cavities), in 2002. Genotyping methods are described in detail in Stapleton (2005).

Statistical analyses.—We plotted bird locations and used AutoCAD to calculate distances (Autodesk 2000). Differences in distance from nest box in the pre-laying compared with the laying period were calculated with JMPIN (SAS Institute, Inc. 2000) using a two-tailed matched-pair t-test at the 0.05 significance level. We used GERUD1.0 (Jones 2001) to calculate the minimum number of extra-pair sires within a given brood, based on the maximum number of unique paternal alleles present in all offspring of the brood. Values reported in the results are means ± SE.

RESULTS

All four female Tree Swallows were tracked until at least 2 days after the first egg was laid (i.e., until at least day +2; Table 1). Due to difficulties in locating precise roosting sites, we used last-known location at night and first-known location in the morning as a proxy for roosting location (i.e., distance and direction from nest box). Radio-tracking effort, calculated for each individual, varied due to individual differences in first egg dates (range = 49.7–79.3 hr, 11–18 days; Table 1). Dates are reported as negative and positive integers, with 0 representing the first egg day.

Movement.—There was a tendency for females to be detected farther from the nest box in the pre-laying period (mean 661 ± 200 m) than in the laying period (225 ± 200 m; matched-pair t-test: $t_{1,3} = -2.80$, $P = 0.068$). Two females (STA3 and HUW2; Table 1) tended to remain in or near their nest boxes, one female (SRBP1) was commonly found at intermediate distances from her nest box, and one female (NBF2) routinely roosted >2500 m from her nest box.

The female nesting at NBF2 was detected the farthest from her nest box. Although her nest box was within 200 m of three other Tree Swallow grids, she was frequently located in the evenings near the SRB grid, which was approximately 2,300 m distant. NBF2 did not roost on her grid until day +3 (Table 1). Prior to that, she was detected >2,500 m from her nest box on the evenings of day −6 and day −1. SRBP1 female was detected off her grid early in the pre-laying period at distances of ≤883 m (day −4), but then she stayed close

TABLE 1. Summary information for four Tree Swallows radio-tracked in May 2002 at Queen's University Biological Station, Ontario, Canada. Day (relative days tracked) was relative to the first egg date (day 0). Location of a female during the pre-laying and laying periods was designated either as "on" (≤100 m from nest box) or off (≥101 m from nest box) a nest-box grid.

Female	Age[a]	First egg date	Relative days tracked	Pre-laying (on/off)[b]	Laying (on/off)[b]	Clutch size	No. EPO[c]	Min. no. EP[d] sires	EPO in brood (%)	Hr tracked
NBF2	SY	23 May	−6 to +4	0/5[e]	1/4	5	1	1	20	49.7
SRBP1	SY	26 May	−9 to +2	2/7	3/0	6	1	1	17	57.2
STA3	ATY	22 May	−5 to +5	2/2[e]	5/0	5[f]	≥1[g]	1	≥33	47.9
HUW2	ASY	26 May	−11 to +2	7/4	2/0[h]	5	3	1	60	75.3

[a] SY = second year, ASY = after-second-year, ATY = after-third-year.

[b] "On" = the number of times a female was detected ≤100 m from her nest box (i.e., on or very near the nest grid) during each last nightly check; "off" = the number of times a female was either detected ≥101 m from her nest box or no signal was obtained from the nest grid during each last nightly check.

[c] Extra-pair offspring.

[d] Minimum number of extra-pair (EP) sires (calculated in GERUD1.0), based on the number of unique paternal alleles.

[e] No telemetery information recorded for females NBF2 and STA3 on days −5 and −4, respectively during the pre-laying period.

[f] Two nestlings were not genotyped (one nestling disappeared from the nest; one nestling did not yield DNA).

[g] Social male not captured; presence of extra-pair young is based on number of unique paternal alleles.

[h] No telemetry information recorded for female HUW2 on day +1 in laying period.

to the grid for the remainder of the tracking period. From the evening of day −2 until the end of tracking (day +3), she was never detected >72 m from her nest box and seemed to be roosting near the grid (Table 1). STA3 female showed very little movement and was not detected off her grid between day −1 and day +4, her last egg day (Table 1). Her maximum detected movement was 1,646 m on the morning of day −2. HUW2 female showed the least amount of movement and was never detected off her grid between day −6 and day +2 (Table 1).

Paternity.—All four focal females produced at least one extra-pair offspring (Table 1). For one female, we were unable to catch her social mate. In this case, we used number of paternal alleles per locus in the offspring to estimate the minimum number of sires represented in the brood (i.e., greater than three unique alleles at a single locus in offspring indicates more than one sire). We were unable to assign any extra-pair mates for any of the four focal females, despite our success at sampling the majority of males using nest boxes in this population.

DISCUSSION

Last-known locations at night combined with first-known locations in the early morning indicated that individual female Tree Swallows in this population do not return to the same roost site night after night. In addition, individuals varied with respect to how far away from their nest sites they roosted. Although two females (HUW2 and STA3) were rarely detected >50 m from their nest boxes, one female (NBF2) was routinely detected up to 2 km from her nest box. There was a strong tendency for females to remain closer to their nest boxes in the laying period than in the pre-laying period. Overall, our results indicate that movement patterns of Tree Swallows differ both within and among individuals. These results are in accordance with those of a recent study on a Wisconsin population of Tree Swallows (Dunn and Whittingham 2005), in which four females that were tracked to their roosting sites over several evenings prior to egg laying did not always use the same roost on subsequent nights. Furthermore, although these females all nested within 0.5 km of each other, their individual roosting sites defined an area of at least 103 km^2. Together, these results highlight the importance of continued studies away from the area immediately surrounding the nest site, particularly for passerines such as Tree Swallows that spend considerable time away from their territories during the breeding season.

The tendency for some female Tree Swallows to roost away from their nest site during their fertile period has implications with respect to extra-pair mating. Unlike many other passerines, most extra-pair sires among Tree Swallows do not seem to be neighboring males (Dunn et al. 1994, Kempenaers et al. 1999, Kempenaers et al. 2001). In our study population, we were able to identify extra-pair sires for 49% of extra-pair young (Stapleton 2005), a pattern consistent with results of previous studies (Dunn et al. 1994, Kempenaers et al. 1999, Kempenaers et al. 2001). Dunn et al. (1994) suggested that female Tree Swallows obtain their EPCs at roosting sites. Although we were unable to directly observe birds roosting away from their nest boxes, our data did allow us to determine whether or not a given female spent the night at her nest box. Initially, we had predicted that the extra-pair sires for a given brood would be neighboring males if the female tended to roost on or very near her nest-box grid; however, although all females in this study produced extra-pair young, we were unable to identify extra-pair sires for any of the four focal females, despite having sampled most of the neighboring males. Thus, whether or not a female roosted away from her nest box or tended to remain nearby did not affect whether she produced extra-pair offspring sired by neighboring males in our small sample of radio-tagged birds.

Our study provides additional evidence that movements of female Tree Swallows are extensive and variable during their fertile period (see Dunn and Whittingham 2005). The main difficulty with our study was our inability to consistently locate the Tree Swallows fitted with transmitters. Despite these difficulties, we encourage future telemetry studies coupled with parentage analyses on Tree Swallows, particularly in areas with flat topography and adequate vehicular access to aid in tracking these birds over their relatively large home ranges during the breeding season.

ACKNOWLEDGMENTS

We would like to thank C. A. Dale for her excellent assistance in the field and W. F. Connor for assisting with field work and the GPS/GIS aspect of the project. D. J. Mennill provided advice and guidance on harness construction. We are grateful to J. T. Lifjeld, D. L. Neudorf, L. M. Ratcliffe, D. W. Winkler, T. E. Steeves, and two anonymous reviewers for comments that improved earlier versions of this manuscript. All methods in this study were approved by the Queen's University Animal Care Committee under permit # RobertsRJ-040. Funding was provided through grants from the American Ornithologists' Union (MKS), the Society for Canadian Ornithologists (MKS), Queen's University (MKS), and an NSERC equipment grant and operating grant (RJR).

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EFFECTS OF PRESCRIBED FIRE ON CONDITIONS INSIDE A CUBAN PARROT (*AMAZONA LEUCOCEPHALA*) SURROGATE NESTING CAVITY ON GREAT ABACO, BAHAMAS

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ABSTRACT.—Cuban Parrots (*Amazona leucocephala*) on the island of Great Abaco in the Bahamas forage and nest in native pine forests. The population is unique in that the birds nest in limestone solution holes on the forest floor. Bahamian pine forests are fire-dependent with a frequent surface fire regime. The effects of fire on the parrots, especially while nesting, are not well known. We measured ambient conditions inside a cavity characteristic of the Cuban Parrot's Abaconian population as a prescribed fire passed over it. Cavity conditions were relatively benign; although temperatures immediately outside the cavity rose to >800° C, inside temperatures increased only 5° C at 30 cm inside the entrance and 0.4° C at the cavity floor (cavity depth was ~120 cm). CO_2 levels briefly rose to 2,092 ppm as the flames passed, but dropped to nearly ambient levels approximately 15 min later. Smoke levels also were elevated only briefly, with 0.603 mg of total suspended particulates filtered from 0.1 m^3 of air. Smokey conditions lasted approximately 20 min. *Received 23 September 2005, accepted 5 May 2006.*

In the Bahamas, the Cuban Parrot (*Amazona leucocephala*) currently occurs only on the islands of Great Abaco and Great Inagua. The Bahamian populations of Cuban Parrots are often recognized as a subspecies (*Amazona leucocephala bahamensis*). Regardless of taxonomic rank, the Great Abaco population is distinct because the parrots nest in the ground, exploiting small solution holes in the exposed limestone bedrock found in stands of Caribbean pine (*Pinus caribaea* var. *bahamensis*)—a forest type known locally as "pineyards." This ground-nesting behavior is unique, as all other populations of Cuban Parrots are known to nest in tree cavities. Pine seeds and fruit of other pineyard plants are important food sources for the parrots on Great Abaco during the breeding season (Attrill 1981, Snyder et al. 1982). Bahamian pineyard ecosystems are fire-dependent: frequent fires suppress competing broad-leaved vegetation, remineralize nutrients bound in litter, and prevent fuel buildups that increase the risk of greater fire intensity when accidental fires occur. In the absence of fire, broad-leaved forest species eventually outcompete and replace the overstory pines. In analogous pine forests in southern Florida, suppression of fire resulted in forest succession to broad-leaved vegetation in as few as 25 years (Robertson 1955, Loope and Dunevitz 1981). Fires have been occurring in Great Abaco pineyards every 3 to 5 years since at least the late 1700s (H. D. Grissino-Mayer unpubl. data). Human activities are currently the most frequent sources of ignition, although lightning-ignited fires do occur and their frequency is probably underestimated.

Prescribed fire has become a popular management tool in many protected areas containing fire-dependent vegetation. Currently, the extemporaneous fire management practiced by local Abaconians has been very effective in maintaining the pineyards. Future fire management in the Bahamas will likely depend more on prescribed fires lit by trained professionals as land-use changes complicate fire-management situations. The judicious application of prescribed fire as a resource management tool requires knowledge of fire impacts, both direct and indirect, on ecosystem properties. Although the relationship between fire and pineyard vegetation is relatively clear, the impact of fire on pineyard wildlife, especially parrots, is not as well known. The ground-nesting behavior of the Abaconian

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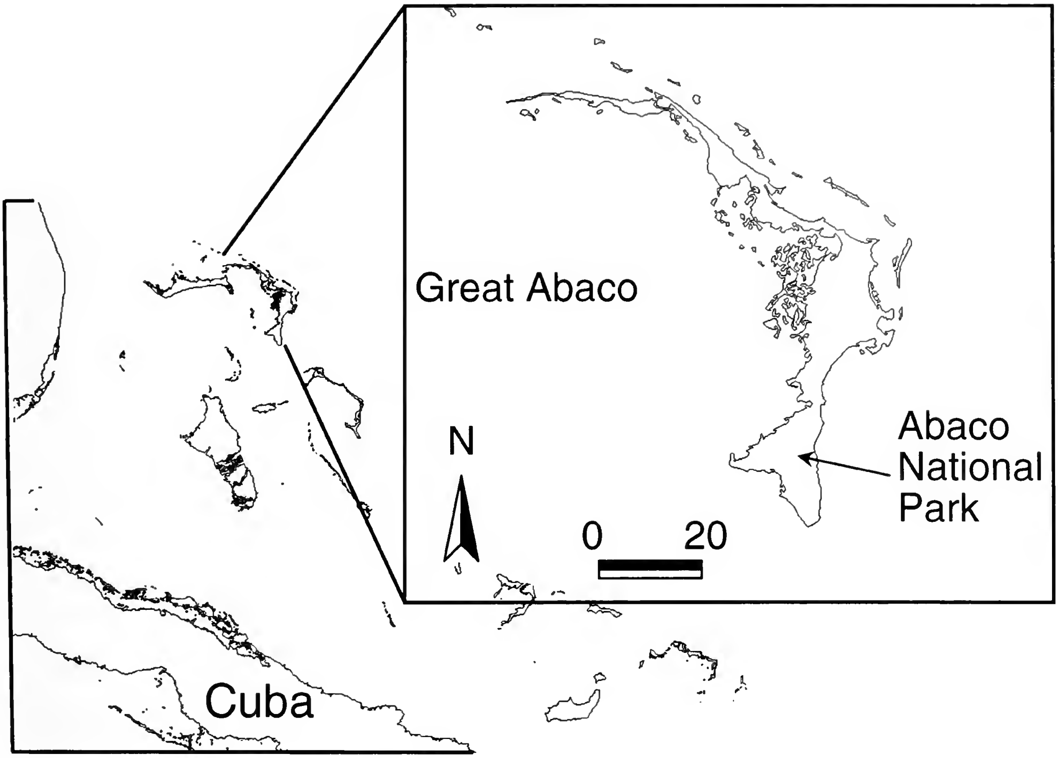

FIG. 1. Location of the island of Great Abaco and Abaco National Park within the Commonwealth of the Bahamas.

population raises several important questions regarding the ways in which fires might affect nesting parrots.

Fire can impact parrots both indirectly and directly. Indirect effects are mediated primarily through vegetation and subsequent impacts on parrot food resources and nesting cover. Direct effects would likely be most important during the nesting season. A passing fire might result in increased temperatures, smoke, and CO_2 levels inside the nesting cavity that could stress or kill parrot nestlings or adults reluctant to abandon the nest. Herein, we report the ambient conditions inside a limestone cavity characteristic of Cuban Parrot nest sites as a prescribed fire passed over it. Conditions are reported as means ± SD.

METHODS

The study site bordered Abaco National Park (ANP; 26° 2′ N, 77° 15′ W) in the southern portion of the island of Great Abaco, Bahamas (Fig. 1). ANP was established in 1994 by The Bahamas National Trust and encompasses 8,300 ha. The habitat consists of pineyard vegetation along with some tropical dry forest known locally as "coppice." A forest inventory we conducted in the vicinity of the experimental area revealed that pine trees now occupying the park are growing in even-aged stands. Mean tree height was 16 m ± 0.6, mean diameter at breast height was 18.6 cm ± 1.81, and mean density was 364 ± 273 trees/ha.

On 31 October 2004, a crew led by personnel of The Nature Conservancy lit a prescribed fire in Abaco National Park as a training exercise for Bahamian fire fighters and resource managers. The crew used drip torches to ignite the fire at 13:00 EST under moderate weather conditions: ~1 m/sec wind speed, 56% relative humidity, and high levels of fuel moisture resulting from rainfall the previous evening. The area burned was a ~10 ha block bounded by former logging roads and a highway. Although the site's exact fire history was unknown, fuel loads were typical of areas that had not burned for about 3 yr. The study plot was embedded in an area of high-density parrot nesting activity (Gnam and Burchsted 1991, Stahala 2005), with an active colony <1 km distant. The fuel loads and stand structure in both the study area and the nearby colonies were similar.

Prior to ignition in the area to be burned, we located a solution hole characteristic of those used by parrots as nesting cavities (Snyder et al. 1982, Gnam 1990). This cavity entrance was ~30 cm in diameter, within the diameter range previously reported for parrot cavity entrances, and was approximately 120 cm deep, also within the range reported for parrot cavities (124.2 ± 55.4; Gnam 1990). The floor was dry and contained a small heap of dried grass—evidence of vertebrate activity within the cavity. In order to measure temperatures inside the cavity, we placed two type-T thermocouples read by Hobo dataloggers (Hobo Pro Series, Onset, Inc., Bourne, Massachusetts) on the cavity floor, and suspended another thermocouple 30 cm inside the entrance. As the fire passed over the cavity, an infrared camera (S60, FLIR, Inc., Wilsonville, Oregon) was used to measure ground surface temperatures outside the cavity.

Inside the cavity, we also measured CO_2 concentration and total suspended particulate density by sampling air through a 4-m-long, 5-mm-diameter copper tube with the end placed 10 cm above the surface of the cavity floor. A particulate matter (PM) 2.5 filter (collects particulate matter ≥ 2.5 μm) was attached to the tube tip inside the cavity. At its other end, the tube was connected to an air pump set at a maximum flow rate of 1.5 l/min. We measured CO_2 levels with an infrared gas analyzer (EGM4, PP Systems, Inc., Amesbury, Massachusetts); the air flow rate was measured simultaneously with a mass flow controller (Top-Trak 822-OV1-PV1-V1, Sierra Instruments, Inc., Monterey, California). The output of the gas analyzer and mass flow controller were measured every second and stored as 1-min averages by a datalogger (CR10X, Campbell Scientific, Inc., Logan, Utah). All instruments were placed in a small plastic enclosure. To prevent fire damage, we raked fuel from around the enclosure, then covered it with a U.S. Department of Agriculture Forest Service fire shelter, an aluminized fiberglass tent designed to shield an entrapped firefighter from radiant energy.

RESULTS

Although a variety of ignition techniques were employed in the area, a low-intensity backing fire arrived at the cavity area at approximately 15:14. The low fuel loads found in the area, coupled with the moderate weather conditions, created short flames (~30 cm high) and a slow rate of spread; the fireline crept along at about 15 cm/min as the fire passed the vicinity of the cavity entrance. The residence time of the fire within 1 m of the cavity entrance was ~15 min. The maximum fire temperature recorded outside the cavity entrance was 803° C. We observed minor temperature changes inside the cavity as the fire passed: a 5° C increase occurred 30 cm inside the entrance, and a 0.4° C increase occurred at the cavity floor (Fig. 2A).

A total of 0.903 mg of suspended particulates was captured on the PM 2.5 air filter after 0.1 m^3 of air had been filtered. Changes in air flow through the filter indicated that smoke accumulation was constant for a brief period, causing a steep, linear decrease in air flow, but then smoke concentration declined toward an asymptote (Fig. 2B). There was little lingering smoke production, as almost no smoldering occurred following passage of the flaming front.

CO_2 levels in the cavity rose sharply when the fire approached the entrance and then dropped sharply as the fire moved past (Fig. 2B). The maximum concentration recorded was 2,092 ppm. Concentrations of CO_2 >2,000 ppm occurred for 5 min, and concentrations >1,000 ppm occurred for 19 min.

DISCUSSION

We observed relatively benign conditions inside the cavity as the fire passed. The magnitude of temperature change caused by the fire was similar to that observed during a typical diurnal cycle in the absence of fire (GPM unpubl. data). Inside the cavity, smoke levels were low, and CO_2 levels rose moderately, but declined quickly as the fire passed. The CO_2 concentrations we observed probably would not have had much effect on parrots: although data on CO_2 effects on birds were not avail-

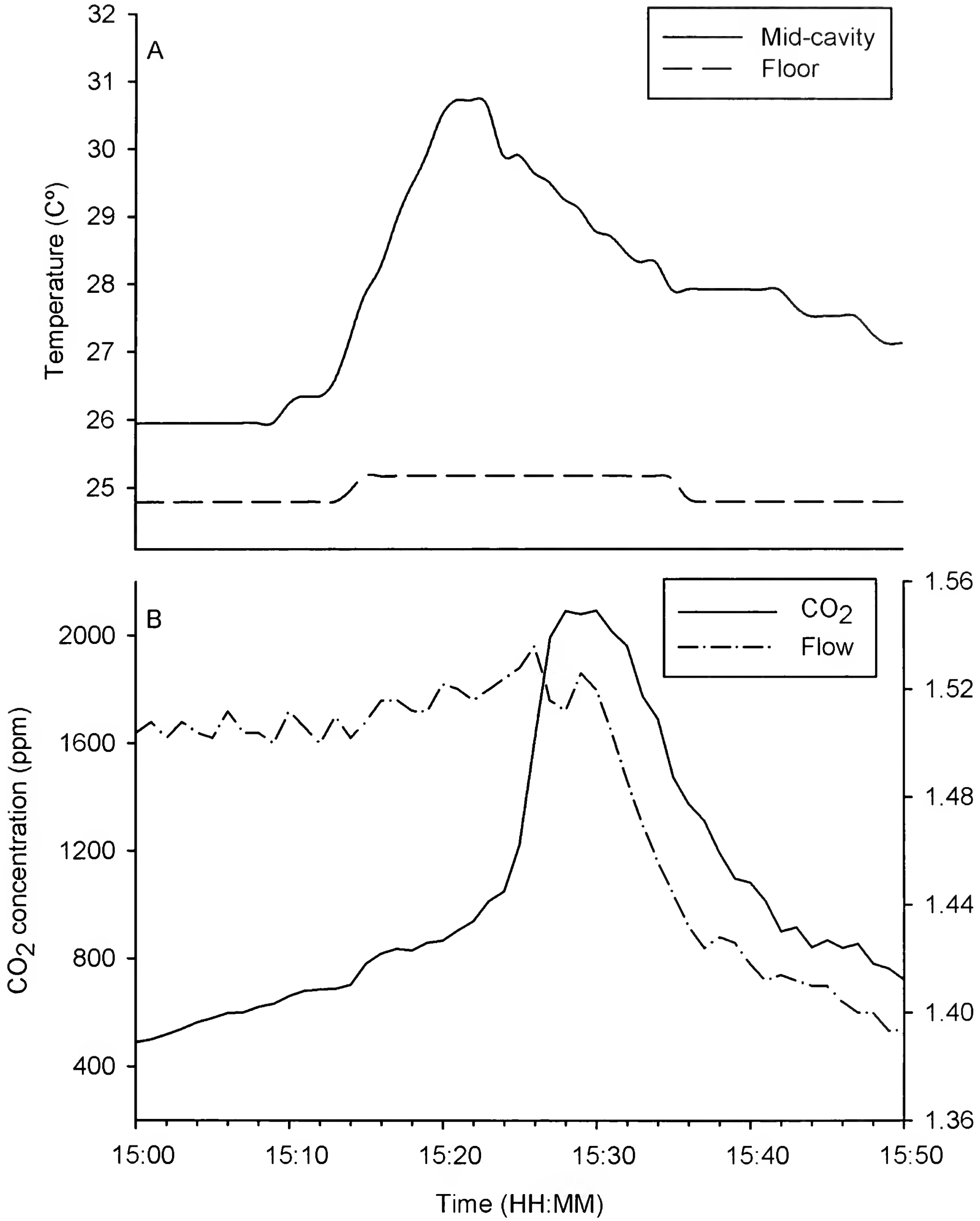

FIG. 2. Ambient conditions inside a Cuban Parrot surrogate nest cavity in Abaco National Park, Great Abaco, Bahamas. (A) Temperatures 30 cm inside the cavity entrance and on the cavity floor 100 cm from the entrance. (B) CO_2 concentration and air flow rate through a particulate filter as a fire passed by the cavity; the flaming front approached the cavity entrance at 15:14 EST and passed at approximately 15:35.

able, the maximum permissible exposure for humans, as determined by the Occupational Safety and Health Administration (1997), is an 8-hr time-weighted average of 5,000 ppm with a short-term (<30 min) exposure limit of 30,000 ppm. Concentrations lower than 15,000 ppm have no detectable effect on people.

Although the tolerance of Cuban Parrots to CO_2 and smoke is unknown, they are capable of surviving fires while nesting. In 2003, a wildfire passed over 20 occupied nests and did not result in decreased fledging success (Stahala 2005). Another wildfire that occurred in ANP in 2005 resulted in a similar lack of mortality (GPM pers. obs.). Our measurements also provide direct evidence that fire-induced elevations in temperature and CO_2 concentration would cause minimal stress. Although we sampled only a single cavity (thus limiting our sphere of inference), our results are likely representative, given the low fuel loads that are typically found in nesting colonies.

Burning while the birds are actively nesting might have a relatively minor impact on conditions inside the cavity. Nonetheless, the threatened status and restricted range of the ground-nesting population, as well as the ample opportunity to set fires outside the breeding season, indicates that setting prescribed fires when cavities are occupied needs to be considered carefully. The timing of a fire appears to be important, as parrot pairs seem to choose new nesting sites in recently burned areas. Although it appears that reduced cover due to fire has no significant effect on predation rates of nesting parrots (Stahala 2005), unburned patches near nests might attract predators in otherwise burned areas. If this were true, creating firebreaks around colonies to protect parrots from fire might lead to increased parrot mortality and would not be justifiable. While the direct effects of fire on conditions inside a nest cavity of Abaco's Cuban Parrots appear negligible, indirect effects of frequent fires are of paramount importance, mainly because they reduce fuel loads and fire intensities and are critical for maintaining pineyard ecosystems.

ACKNOWLEDGMENTS

We would like to thank the Friends of the Environment (Bahamas) for providing invaluable logistical support, the Bahamas Department of Agriculture, especially D. Knowles, the Bahamas National Trust, and the U.S. Department of Agriculture Forest Service International Program for facilitating our research. Three anonymous referees provided valuable comments that improved this manuscript. K. Smith provided logistical support and assisted with manuscript preparation.

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The Wilson Journal of Ornithology 118(4):513–526, 2006

UTILITY OF OPEN POPULATION MODELS: LIMITATIONS POSED BY PARAMETER ESTIMABILITY IN THE STUDY OF MIGRATORY STOPOVER

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ABSTRACT.—Open population models using capture-mark-recapture (CMR) data have a wide range of uses in ecological and evolutionary contexts, including modeling of stopover duration by migratory passerines. In using CMR approaches in novel contexts there is a need to determine the conditions under which open population models may be employed effectively. Our goal was to determine whether there was a simple *a priori* mechanism of determining the conditions under which CMR models could be used effectively in the study of avian stopover ecology. Using banding data (n = 188 capture histories), we examined the challenges of using CMR-based models due to parameter inestimability, adequacy of descriptive power (Goodness-of-Fit, GOF), and parameter uncertainty. These issues become more apparent in studies with limited observations in a capture history, as is often the case in studies of avian stopover duration. Limited sample size and sampling intensity require an approach to reducing the number of fitted parameters in the model. Parameter estimability posed the greatest restriction on the utility of open population models, with high parameter uncertainty posing a lesser challenge. Results from our study also indicate the need for >10 observations per estimated parameter (approximately 3 birds captured or recaptured per day) to provide a reasonable chance of successfully estimating all model parameters. *Received 13 July 2005, accepted 20 May 2006.*

Migratory birds frequently use stopovers to complete migration successfully between their breeding and wintering grounds. Stopover sites provide refuge from predators, protection against inclement weather, and food resources to allow fat deposition to fuel migratory flight. It is thought that many migrating passerines cannot store enough fat to complete their migration in a single transit, but must refuel by foraging at stopover sites along their routes (Dunn 2001, Schwilch and Jenni 2001). Providing evidence for the use of stopover sites for refueling, Moore and Aborn (2000) documented increased activity patterns and differential habitat use by lean versus fat migrants. Lean migrants needing to refuel may stay longer at stopover sites than fat migrants (Moore and Kerlinger 1987, Yong and Moore 1997), and the rate of mass gain also may affect stopover duration. The length of time that migrants stay at stopover sites will affect the total duration of migration and may affect the ability of birds to obtain quality territories. Species-specific stopover patterns may reflect both intrinsic characteristics and ecological factors associated with individual stopover sites (Kaiser 1999). Schaub et al. (2001) argue for accurate estimates of stopover duration to test models of optimal migration strategy, specifically the trade-off between time spent in flight or at stopovers.

Although the importance of *en route* migratory stopover sites is well recognized (Moore 2000, Petit 2000, Sillett and Holmes 2002, Heglund and Skagen 2005), all sites are not equal. Mehlman et al. (2005) recommend that important stopover sites be identified based on the relative migrant abundance, the availability of resources that allow birds to replenish fat reserves, and the location of the site relative to other sites and ecological barriers. However, specific criteria for assessing, and statistical approaches for comparing, sites have not been established. Furthermore, there is a recognized need for research on how sites differ by season, species, and species demography (Mehlman et al. 2005, Partners in Flight Research Working Group 2002).

Since the mid-1980s, numerous researchers have described the basics of the stopover ecology of migratory landbirds at individual sites along the northern coast of the Gulf of Mexico

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(Moore and Kerlinger 1987, Moore et al. 1990, Kuenzi et al. 1991), the New England coast (Morris et al. 1994, 1996; Parrish 2000), the Great Lakes coasts (Jones et al. 2002, Bonter 2003), and in western states (Winker et al. 1992, Finch and Yong 2000). Most of these studies provide simple analyses of stopover duration based on recapturing banded birds. Calculating the amount of time lapsing between the first capture and the last recapture (Cherry 1982) has been the traditional method of estimating stopover duration at a given site; however, including only recaptured birds provides conservative estimates of stopover duration because birds not recaptured have not necessarily left the field site. If only recaptured birds are used in analyses (regularly <5% of all banded migrants are recaptured), this simple approach might provide a biased view of site use because >95% of migrants are excluded from analyses.

The limitations of the minimum stopover approach have resulted in the suggestion that open population models based on capture-mark-recapture (CMR) data be used to estimate stopover duration (Lavee et al. 1991, Holmgren et al. 1993, Kaiser 1995, Schaub et al. 2001). The Pradel (1996) extension of the Cormack-Jolly-Seber (CJS) models allows for a range of models of the probabilities of animal capture, arrival, and departure within each interval of a given study period. A number of useful statistics may be derived from the stochastic models, including mean time animals are present in the study area, mean capture probability, and temporal patterns of arrival, departure, and population size. These models also could allow meaningful comparisons of several stopover characteristics among sites.

Although the assumptions used in deriving open population models are widely known (e.g., Pollock et al. 1990, Cooch and White 2005), the conditions under which these models can be used are rarely discussed. Characteristics of the data (i.e., capture/recapture histories)—especially sample size, number of temporal sampling intervals available, recapture/resighting/recovery rate, etc.—may greatly impact the potential usefulness of these models. To use a given open population model, first all the model parameters must be estimated. Typically, parameter estimates are obtained using numerical maximum likelihood methods; characteristics of the capture history and the model's mathematical structure will determine the number of parameters that can be reliably estimated. Parameters that are inestimable due to limitations of a given capture history are extrinsically non-identifiable (McCullagh and Nelder 1989, Viallefont et al. 1998). Capture histories that involve long periods of time, particularly those with relatively few captures and/or recaptures, often prevent successful estimation of all parameter values; the resulting extrinsic non-identifiability of parameters either precludes the use of open population models or requires reducing the number of parameters.

One approach to reducing the number of parameters that must be fitted for a given model is to pool observations over several consecutive observation periods (e.g., Schaub and Jenni 2001, Schaub et al. 2001). However, pooling may bias the parameter estimates and preclude comparing models with different pooling intervals (Hargrove and Borland 1994, Morris et al. 2005b). The difficulty associated with the need to establish this basic temporal interval has been recognized in the paleontological literature (Connolly and Miller 2001, Xu et al. 2005), where it has been addressed by determining whether or not analysis results remain consistent as the pooling interval is changed. Additional detailed discussion of pooling and its effects appears to be lacking in both the statistical and ecological literature. An alternative to pooling is to use multiple-day constancy (MDC; Fig. 1), which holds parameter values fixed over a given "constancy" interval, thus reducing the number of parameters while retaining all information in the capture history (Morris et al. 2005a). Regardless of the method used to reduce the number of parameters, decreasing the number of parameters in a model will increase the likelihood that all parameters can be successfully estimated, by reducing the incidence of extrinsic non-identifiability.

When using open population models, goodness-of-fit (GOF) tests must be applied to determine whether the models have adequate descriptive power prior to biological applications. Two distinct approaches (analytical tests based on contingency tables and numerical tests based on comparing observed model misfit or deviance to estimates of misfit de-

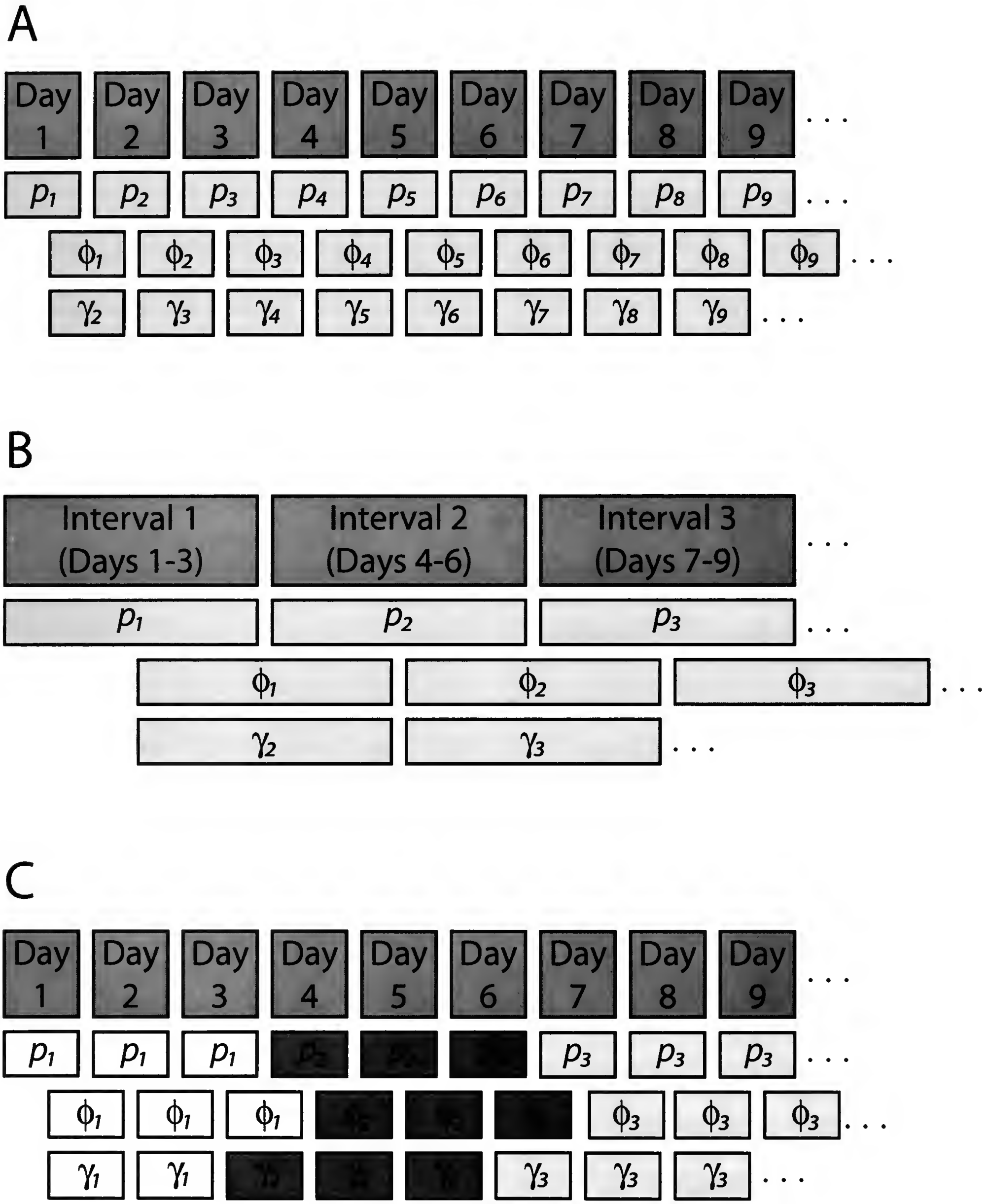

FIG. 1. Open population models may be used to estimate stopover duration by migratory birds by estimating daily rates of capture, arrival, and departure. Large numbers of parameters are required to work with (A) raw data, while both (B) pooled data (3-day pooling interval) and (C) multiple-day constancy (MDC, 3-day MDC interval) provide a reduction in the number of parameters in the open population models fitted to bird banding data. Since limited sample sizes make parameter estimation difficult, some reduction in the number of parameters may allow use of these models with smaller data sets. Both pooling and MDC approaches reduce the number of fitted parameters: p = probability of capture; ϕ = probability that a bird captured on one day remained until the following day (i.e., survival); and γ = probability that a bird captured on one day was there the day before (i.e., seniority). Pooling, however, loses information from multiple captures in the same interval, whereas MDC retains information on all captures. Figure adapted from Morris et al. (2005a).

rived from simulations) have been used to determine whether open population models fit the data. Once the most complex model passes the GOF test, selection of the most appropriate model (of those nested within this most complex model) for the data using Akaike's Information Criterion (AIC) can occur. Even when models can be chosen and fit, the variances of parameter estimates obtained from open population models may be too large for the estimates to be useful. The coefficient of variation (CV; the standard deviation of the estimate/the value of the estimate × 100) may be used to assess the potential utility of stopover estimates. A low CV is necessary for effective comparison of statistical measures among species, locations, and/or time periods. However, little attention has been paid to the dependence of the CV on the characteristics of the capture history.

In this study, we examined capture histories from migration banding data to determine the utility of open population models for estimating avian stopover duration. We used a large number of field capture histories (n = 188) from migration banding datasets rather than relying on computer simulations. Whereas computer simulations would provide greater control over parameters, we wanted to be sure to cover a wide range of natural conditions represented by empirical data. Specifically, we were interested in determining how data characteristics affect parameter estimability (through extrinsic non-identifiability), the ability of models to pass GOF tests, and the CV of stopover duration estimates. Estimating the range of sample sizes and recapture rates to which open population models can be fitted may help us determine whether these approaches are appropriate for a particular capture history. To that end, our results indicate the conditions under which open population models can be used effectively with banding data.

METHODS

Data collection.—Migrating birds were captured in mist nets at Appledore Island, Maine (1996–2002); Star Island, New Hampshire (1999 and 2000); and Hamlin Beach State Park, near Rochester, New York (1999 and 2000). Mist nets were operated daily during the spring and fall migration seasons except during inclement weather. All birds captured or recaptured were transported to a central location for banding and data collection.

For species with a sample size >50 individuals in a single season, we created a capture history that indicated whether any one individual was captured on a given day. Using this capture history, we calculated minimum stopover by subtracting the date of first capture from the date of final capture, following Cherry (1982). Additionally, we calculated a variety of descriptive statistics that were used for discriminant function analyses (see below).

Capture-mark-recapture.—The first step in the analysis was to determine the most complex model for which all parameters could be estimated. Numerical maximum likelihood methods were used to fit Pradel's (1996) extension of the CJS open population models to each capture history. Pradel's model requires estimation of sighting (p = probability of capture), seniority (γ = probability that the bird was present at a stopover site during the previous day), and survival (ϕ = probability of remaining at a stopover site until the next day). We considered time-dependent open population models with MDC intervals (Morris et al. 2005a) ranging from 1 to 7 days. In the MDC approach to time-varying parameters, the parameters are fixed over the MDC interval. However, all captures and recaptures within and between MDC intervals have an influence on the likelihood function and, hence, the parameter estimates. Each of these time-dependent models (in which sighting, survival, and seniority probabilities were all free to vary from one constancy interval to the next) was fitted to the capture history, and the number of extrinsically non-identifiable parameters was identified using an estimate of the rank of the Hessian matrix (Viallefont et al. 1998). Rank deficiency in the Hessian matrix was estimated by using finite-difference methods, and then tested using the singular value decomposition method (Viallefont et al. 1998). Rank deficiency was taken as indicating extrinsic parameter non-identifiability in a model. While some parameters in Pradel's extension of the CJS model are non-identifiable due the model's structure (i.e., intrinsic inestimability), this form of inestimability is part of the model, and does not negatively impact its further use. We are concerned here with extrinsically inestimable parameters in banding data. Inestimability makes it difficult to use either the Schaub et al. (2001) formulation of the stopover duration or the more recent estimate put forward by Efford (2005). Although Efford's approach appears simpler than that of Schaub et al. (2001), it still requires an estimate of the distribution of arrival times, thus necessitating the estimation of the same number of parameters (See Efford's equation 5 and discussion). To be useful in estimating stopover duration (Schaub and Jenni 2001, Schaub et al. 2001), all intrinsically estimable parameters in a model had to be completely identifiable, so those capture histories with non-identifiable parameters due to the structure of the data in all MDC intervals tested were judged unusable for further analysis.

We used software written by HDS and DAL using MATLAB (The MathWorks, Inc. 1992) to implement Pradel's population growth rate (PGR) method (Pradel 1996). We compared the performance of our software to that of MARK (White and Burnham 1999, Cooch and White 2005) and SURGE (Lebreton et al. 1992, Pradel and Lebreton 1993, Cooch et al. 1997); it produced identical results for a number of capture histories, both from our data and from example files distributed with MARK. When using very sparse data, our software and SURGE had similar convergence properties, with results depending less on sample size than they did in MARK, which may be attributable to differences in the particular link function (the default choice) we used in MARK (Cooch and White 2005); this particular difference in performance was not investigated in depth.

Since capture histories included a range of sample sizes and durations, comparing capture histories required a time-invariant measure of sampling intensity. We used the number of observations (sum of all capture and recapture events) per estimated parameter in a 7-day, time-dependent MDC model as the measure of observations per parameter. The 7-day MDC model had the lowest number of parameters of any model used in the estimability determination procedure discussed above. We divided the capture histories into three categories, based on the number of observations (#) per estimated parameter: (1) $2 < \# \leq 5$, (2) $5 < \# \leq 10$, and (3) $\# > 10$. Our highest category (>10 observations per parameter) roughly corresponds with three birds of that species captured or recaptured per day. This categorization allowed us to examine the dependence of estimability on the ratio of observations to parameters, and does not require that the sampling intervals used in a study be in units of days.

Capture histories were tested for GOF by assessing the ability of time-dependent (i.e., the most complex) models to fit the data. Both analytical tests (based on contingency tables) and numerical tests (based on parametric bootstrap procedures) have been used in conjunction with CMR models. The first approach is to use contingency tables to test whether assumptions of the open population models are violated. Specifically, contingency tables are used to test the assumptions that each marked animal in the population at time t has (1) the same probability of recapture, and (2) the same probability of survival (Pollock et al. 1990). Several variations on these tests have been incorporated into the programs RELEASE (Lebreton et al. 1992, Burnham et al. 1987), MARK (White and Burnham 1999), and U-CARE (Choquet et al. 2005). The contingency tables can be pooled to produce an overall chi-square statistic for the capture history as a whole, as well as testing specific hypotheses about violations of model assumptions. When faced with sparse data, the contingency tables may be pooled to improve their performance, particularly when the number of expected outcomes in one or more categories of the contingency table is very low. Pooling contingency tables, however, does not always result in tables with enough entries in each cell to be useful. All of our capture histories that had estimable models for MDC intervals of ≤ 7 days were submitted to GOF testing using the contingency table methods in U-CARE (Choquet et al. 2005).

The second alternative is to use numerical simulations to determine whether the observed model deviance is consistent with the deviance distribution obtained by using the model in a parametric bootstrap procedure (also called a Monte Carlo simulation). The model deviance is the difference between the observed log-likelihood and the log-likelihood for a "saturated" model, and it serves as a model's measure of fit. In such a procedure (as implemented in MARK and our software), the model is used to generate a series of simulated capture histories of the same size as the original capture history. The model is fit to each of the simulated capture histories in turn, and a confidence interval for the deviances observed over the simulated data is obtained. If the observed deviance is high (above the 95% upper bound of the simulation deviances), then it may be possible to continue the analysis by computing an estimated variance inflation factor ($\hat{c}$) and using this to adjust the statistics of model choice (White 2002, Cooch and White 2005). Data sparseness also affects this parametric bootstrap approach to GOF testing because the model must be fit to the simulation data during the estimation of the range of deviances. Each capture history was tested for GOF at the lowest MDC interval for which the model parameters were identifiable, using software written by HDS and DAL. Parameter identifiability was monitored during the GOF testing procedure, as it also poses a problem when conducting Monte Carlo simulations. Similarly, capture histories exhibiting evidence of a lack-of-fit (i.e., those with deviances outside the 95% confidence intervals from the simulations) over all seven intervals were not subjected to further analysis. We did not make use of the $\hat{c}$ estimation procedure (White 2002, Cooch and White 2005), as it turned out that only two capture histories fell into this category of results.

After a time-dependent model was shown to exhibit GOF, we compared competing models to determine which model was optimal for producing stopover estimates. Model selection compared all prospective models over several MDC intervals for each capture history, beginning with the smallest MDC interval that passed GOF. We excluded prospective models that had both constant seniority and survival because they predict a population size that is constant or monotonically increasing or decreasing. Based on field observations, we know that during the migration period the population present at a stopover site increases to a maximum value and then declines to zero, making any model predicting constant population size or a monotonic pattern of change in population size biologically unreasonable (see Burnham and Anderson 1998 for a discussion of the exclusion of biologically unreasonable models). The lowest AIC_c value indicated the most appropriate model for a given capture history, thus determining the appropriate MDC interval and whether each parameter was constant or time-dependent. In addition to determining which model was the most appropriate, the AIC_c score was used to assign a relative AIC_c weight (w) to each model, which reflects the relative probability that each model is correct. If the AIC_c weight of the chosen model was <0.95, we also included additional models with relatively high AIC_c weights. Thus, the number of models included was determined by a cumulative AIC_c weight of 0.95, so that all models with a reasonable chance of being correct were considered. We used a bootstrapping procedure to determine the total stopover duration estimate and the standard deviation of this estimate (following Schaub et al. 2001).

Schaub et al. (2001) present a derivation of the expected total stopover duration calculated as a daily value; we report the average total stopover duration over the migration season. In our method, the daily stopover is weighted by the estimated probability of arrival times, using the estimated population growth rate as presented by Pradel (1996). Efford (2005) argues that the total stopover duration (Schaub et al. 2001) produces an overestimate of the actual duration. Efford (2005) advocates using a weighted average of Schaub et al.'s "stopover-after" estimate using a weighting derived from Schwarz and Arnason's (1996) estimates of the distribution of arrival times (Equation 5 in Efford 2005). We also present the stopover-after statistic, again weighted using the estimated population growth rate as derived from Pradel (1996). Conceptually, this approach is the same as that presented by Efford, although the computations may differ slightly, as the Pradel (1996) parameterization of the problem differs from that used by Schwarz and Arnason (1996).

In addition to having adequate descriptive power and being estimable, the chosen model must yield a useful statistic for comparisons. The coefficient of variation (CV) was used to determine usefulness of the total stopover statistic estimated for each species in each season. CV was calculated by dividing the standard error of the total stopover estimate by its mean and multiplying by 100. In this study,

TABLE 1. Summary of the utility of open opulation models in three categories representing the number of observations (#) per estimated parameter for a given capture history from avian banding data. To be applicable, models had to have estimable parameters and pass goodness-of-fit (GOF) testing. As the number of observations per parameter increased, the number of capture histories that could be analyzed using open population models also increased. Parameter inestimability in both model fitting and GOF testing poses the greatest impediment to the use of open population models at these sample sizes. Bird banding data were collected during spring and fall migration on Appledore Island, Maine (1996–2002); Star Island, New Hampshire (1999–2000); and Hamlin Beach State Park, New York (1999–2000). The banding data were used to create capture histories, which indicate whether and individual bird was captured on a particular day; a separate capture history was created for each bird species for which there were >50 captures at a single location during a specific season.

	No. observations per estimated parameter		
Capture histories that:	$2 < \# \leq 5$ (n = 42)	$5 < \# \leq 10$ (n = 81)	<10 (n = 65)
Had inestimable parameters	24 (57%)	29 (36%)	16 (25%)
Were inestimable in simulation GOF	15 (36%)	30 (37%)	6 (9%)
Failed simulation GOF	0 (0%)	0 (0%)	2 (3%)
Failed U-CARE "transients" test	0 (0%)	1 (1%)	4 (6%)
Had an applicable model	3 (7%)	21 (26%)	37 (57%)
Had a CV <50% in total stopover duration[a]	1 (2%)	7 (9%)	15 (23%)
Had a CV >50% in total stopover duration[a]	2 (5%)	14 (17%)	22 (34%)
Had a CV <50% in stopover-after[b]	1 (2%)	9 (11%)	18 (28%)
Had a CV >50% in stopover-after[b]	2 (5%)	12 (15%)	19 (29%)

[a] Total stopover estimates are based on open population models and estimates from stopover duration analysis (SODA) described in Schaub et al. (2001); CV (coefficient of variation) = (SE/mean) × 100.

[b] Stopover-after estimates are based on open population models and estimates using equation 5 from Efford (2005).

only CV values ≤50% were considered useful because comparing different stopover estimates is impossible when CV values are substantially >50%. CV values could, of course, be determined for any estimated parameters in the model; we focus here on the derived statistic (stopover duration) relevant to the study of migration ecology.

Discriminant function analyses.—We used discriminant function analyses to examine which conditions led to estimability of parameters in the original capture history and during GOF testing. We used a range of simple statistics that could be calculated without employing the complex CMR models. The variables included in these analyses were the number of individuals captured, number of days sampled, percent of individuals recaptured at least once, total number of captures and recaptures, total number of recaptures, number of captures per day, median captures per day, recaptures per day, number of days with no captures or recaptures, minimum stopover estimate, standard deviation of the minimum stopover estimate, standard deviation in the number of captures per day, and several measures of capture consistency, which we term "completeness." Completeness is the percentage of days on which there was ≥1 capture event, while "completeness two" refers to the percentage of days with ≥2 capture events. "Recapture completeness" and "recapture completeness two" refer to the percentage of days with ≥1 or ≥2 recaptures, respectively. Backwards stepwise discriminant analyses were performed in SYSTAT 10.2 (SYSTAT Software, Inc. 2002).

RESULTS

We examined the parameter estimability of 1- to 7-day MDC models applied to 188 capture histories representing 34 different species (97 capture histories from fall and 91 from spring migration). Of these, we were able to obtain estimable parameters of a completely time-dependent MDC model for 119 capture histories. The MDC interval at which models could be estimated varied among capture histories. The shortest interval that could be used ranged from 3 to 7 days (3-day n = 15, 4-day n = 22, 5-day n = 40, 6-day n = 21, 7-day n = 21). Parameter estimability was strongly dependent on the number of observations per parameter (Table 1). Estimability also played a large role in the outcome of GOF testing. Relatively few capture histories failed GOF testing in an absolute sense. Five capture histories showed evidence of differences in capture probabilities of previously recaptured individuals relative to new captures (the transience test) in U-CARE, and two had excess deviance in the parametric bootstrap test (simulation GOF). The remaining capture histories that "failed" GOF did so because of parameter inestimability in the bootstrap procedure. In these instances, the models could not be fit reliably to the simulated data (i.e., there were problems with estimability in ≥10% of the simulated capture histories). The ability of models to satisfy the GOF criteria was substantially greater for capture histories in our highest category (>10 observations per parameter) than in those in the other two categories ($2 < \# \leq 5$ and $5 < \# \leq 10$ observations per parameter; Table 1). Data sparseness also affected the contingency tests implemented in U-CARE; 42% ($n = 119$) of the capture histories with estimable parameters produced useful contingency tables, although the percentage varied among our three categories ($2 < \# \leq 5$: 0%, $n = 18$; $5 < \# \leq 10$: 38%, $n = 52$; >10: 61%, $n = 49$).

A discriminant function analysis of all capture histories with >10 observations per parameter produced a moderately effective, statistically significant discriminant function describing parameter estimability (Wilks' $\lambda = 0.53$, $F_{5,59} = 10.41$, $P < 0.001$) with positive loadings on duration, recapture completeness, and median captures per day. There were negative loadings on number of recaptured birds and minimum stopover. To extract biological information from discriminant function loadings, we examined a range of bivariate plots depicting the various loadings. The plots yielded only one clear biological interpretation: capture histories with high minimum stopover duration often had inestimable parameters (Fig. 2). Parameter estimability during GOF testing limited the number of capture histories that could be analyzed; however, a discriminant function analysis to predict parameter estimability during GOF testing of the 49 capture histories that were estimable and had >10 observations per parameter was not significant (Wilks' $\lambda = 0.83$, $F_{4,44} = 2.20$, $P = 0.085$).

Optimal models for the capture histories that passed GOF testing varied in the incorporation of time-dependent parameters and in the MDC interval used in the models. When the AIC_c was used to compare the estimable candidate models, regardless of the number of observations per parameter, 88 viable models were identified for the 61 capture histories. The total number of models exceeded the number of capture histories, as multiple models were considered for some capture histories. For 46 of the 61 capture histories, a single model had an overwhelming AIC_c weight (>0.95), indicating that a unique model was identified. Two alternative models were identified for seven capture histories, three alternative models were identified for six capture histories, and four and six models were identified for one capture history each. Parameters that were time-dependent also varied among the chosen models. All three parameters were time-dependent in 14 capture histories, two parameters were time-dependent in 38 capture histories (p and ϕ: 15; p and γ: 17; ϕ and γ: 6), and a single parameter was time-dependent in 36 capture histories (p: 0; ϕ: 13; γ: 23). The MDC time interval chosen for all 61 capture histories varied from 3 to 7 days (3-day $n = 5$; 4-day $n = 2$; 5-day $n = 18$; 6-day $n = 19$; 7-day $n = 44$). Although 52% of our original capture histories were collected during the fall, 75% of the capture histories with applicable models were collected during the fall.

Estimated total stopover duration values ranged from 0.76 to 17.08 days (Table 2), and the CV values were highly variable (ranging from 13% to 274%). Of the 61 capture histories that were useable after GOF testing, 23 had a total stopover CV of <50% (Table 1). Stopover-after estimates ranged from 0.38 to 10.13 days, which were shorter than the estimates of total stopover. Despite the difference in stopover duration estimates obtained by estimating total stopover and stopover-after, stopover-after had a slightly wider range of CV values than total stopover. CV values for stopover-after ranged from 13% to 365%. Most of the estimates involving CV values of <50% were capture histories from the fall migration season (18 of the 23 estimates for total stopover and 24 of 28 estimates for stopover-after), approximately mirroring the distribution of spring and fall capture histories (75% of estimable capture histories were collected during the fall). These useful estimates were

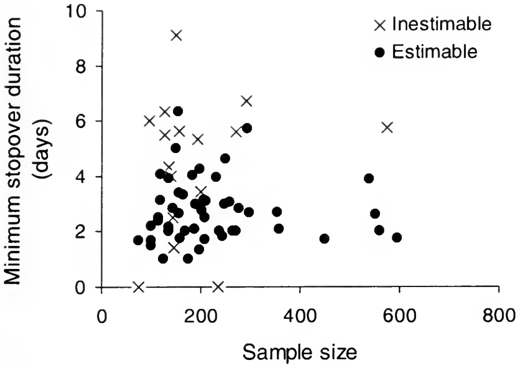

FIG. 2. The relationship between parameter estimability, minimum stopover duration (days), and sample size. Among capture histories of landbird species at migratory stopover sites that had 10 or more (by species) capture events per estimated parameter, those with high minimum stopover duration often had inestimable parameters.

obtained for a variety of species including two vireos, Red-breasted Nuthatch (*Sitta canadensis*), two kinglets, two thrushes, Gray Catbird (*Dumetella carolinensis*), many warbler species, and White-throated Sparrow (*Zonotrichia leucophrys*; Table 2).

DISCUSSION

Our study provided some insights about the conditions under which CMR models can be effectively used to estimate migratory–stopover duration. Dividing the data into three categories based on the number of observations per parameter revealed the importance of the observation:parameter ratio in predicting the utility of CMR models. Models with >10 observations per parameter were estimable and ~62% satisfied GOF testing; most "failures" to satisfy GOF were due to the difficulty of estimating parameters during the GOF procedure when using simulations. If our banding data are representative, then the presence of >10 observations per parameter (roughly three birds captured or recaptured per day) may connote a reasonable probability that CMR models will be useful for characterizing a given capture history.

Although we present analyses based on total number of observations (summed capture and recapture events) per parameter, we also conducted similar analyses using number of individual birds banded per parameter, yielding similar results. The capture histories were also divided into different categories based only on total sample size ($50 \leq n < 100$, $100 \leq n < 150$, and $n \geq 150$). The division by sample size alone was not effective, because sample size is a product of both sampling duration and sampling intensity.

Extrinsic parameter inestimability proved to be the largest impediment to using open population models in our study, affecting both the initial model fitting and GOF testing. The discriminant function analysis revealed that a long minimum stopover (>4 days) was a good indicator that the parameters would not be estimable. Because most birds that are recaptured at stopover sites have minimum stopovers of only a few days, long minimum stopover statistics likely represent multiple birds with unusually long stopovers. Such a scenario would yield a large stopover estimate CV and indicate large biological differences among migrants at a given stopover site. Examining the 16 capture histories with >10 observations per parameter but with inestimable parameters revealed that 3 histories had no recaptures at all and 2 histories had only 2 recaptures. Ten of the capture histories were from three Nearctic-Nearctic migratory species: five White-throated Sparrows (*Zonotrichia albicollis*), four Yellow-rumped Warblers (*Dendroica coronata*), and one Ruby-crowned Kinglet (*Regulus calendula*). Three of the other capture histories represented local breeding species. All of these factors led us to believe that the inestimability in these cases might have been related to heterogeneous migration behavior (either among individuals or subpopulations).

Unlike what we found for parameter estimability, there was no clear single factor explaining parameter inestimability in GOF testing. The discriminant function had low predictive power, with only a 67% chance of correctly predicting the outcome of the GOF test, again indicating the lack of strong factors influencing estimability in GOF. Biological factors related to heterogeneity of the captured specimens (Pollock et al. 1990, Cooch and White 2005) can easily lead to failures of GOF testing. Additionally, there may be statistical reasons for some of the observed failures in GOF testing. The GOF test is based on a Monte-Carlo simulation test run at a 95%

TABLE 2. Results of open population models applied to banding data to estimate stopover duration by migratory birds. Model choice, multiple-day-constancy (MDC) interval, and stopover estimates varied substantially both between and within species. In each case, only the most heavily weighted model is presented. Most models required the use of fairly long MDC intervals, indicating a need to substantially reduce the number of estimated parameters. Many of the resulting stopover duration estimates had high coefficients of variation (>50%), making comparisons difficult. Coefficients of variation were calculated by dividing the standard error of stopover duration, estimated by bootstrapping, by the stopover duration estimate. Bird banding data were collected during spring and fall migration on Appledore Island, Maine (1996–2002); Star Island, New Hampshire (1999–2000); and Hamlin Beach State Park, New York (1999–2000).

Species	Site[a]	Season	Year	*n*	Stopover duration (days)	Chosen model	Total stopover duration estimate (days)[b]	Stopover-after estimate (days)[c]
Traill's Flycatcher (*Empidonax alnorum* and *E. traillii*)	H	Spring	1999	54	14	$p_{.}\ \phi_{7}\ \gamma_{7}$	3.47 ± 2.88	1.14 ± 1.88
Blue-headed Vireo (*Vireo solitarius*)	A	Spring	1996	101	12	$p_{5}\ \phi_{5}\ \gamma_{5}$	**1.73 ± 0.82**	1.33 ± 0.81
Red-eyed Vireo (*V. olivaceus*)	A	Fall	1996	297	41	$p_{.}\ \phi_{.}\ \gamma_{3}$	**4.11 ± 0.62**	**2.22 ± 0.28**
	A	Fall	1997	188	31	$p_{7}\ \phi_{.}\ \gamma_{7}$	**3.42 ± 0.46**	**1.85 ± 0.30**
	A	Fall	1998	258	40	$p_{5}\ \phi_{5}\ \gamma_{5}$	5.37 ± 7.02	3.60 ± 6.87
	A	Fall	1999	231	43	$p_{5}\ \phi_{5}\ \gamma_{5}$	8.37 ± 10.85	**3.71 ± 1.38**
	A	Fall	2000	354	47	$p_{.}\ \phi_{.}\ \gamma_{6}$	**4.30 ± 1.08**	**2.17 ± 0.44**
	A	Fall	2001	277	43	$p_{.}\ \phi_{.}\ \gamma_{3}$	4.97 ± 3.51	**2.38 ± 0.50**
	A	Spring	1996	114	21	$p_{.}\ \phi_{7}\ \gamma_{7}$	1.53 ± 1.19	0.59 ± 0.45
	A	Spring	1998	136	26	$p_{7}\ \phi_{.}\ \gamma_{7}$	1.46 ± 1.03	0.81 ± 0.65
	A	Spring	1999	156	28	$p_{7}\ \phi_{7}\ \gamma_{.}$	1.52 ± 0.89	0.76 ± 0.45
	A	Spring	2000	168	33	$p_{7}\ \phi_{7}\ \gamma_{7}$	11.24 ± 30.81	10.13 ± 30.70
	S	Fall	2000	116	42	$p_{.}\ \phi_{7}\ \gamma_{.}$	**2.30 ± 1.10**	1.22 ± 0.78
Red-breasted Nuthatch (*Sitta canadensis*)	A	Fall	1999	100	48	$p_{.}\ \phi_{7}\ \gamma_{.}$	**7.87 ± 3.46**	3.62 ± 1.82
Golden-crowned Kinglet (*Regulus satrapa*)	A	Fall	2000	100	9	$p_{3}\ \phi_{3}\ \gamma_{.}$	**0.94 ± 0.46**	**0.45 ± 0.22**
	A	Fall	2001	61	18	$p_{.}\ \phi_{.}\ \gamma_{7}$	2.21 ± 1.14	1.22 ± 0.66
	H	Fall	1999	208	24	$p_{5}\ \phi_{.}\ \gamma_{5}$	1.83 ± 1.77	**0.74 ± 0.28**
	H	Fall	2000	450	28	$p_{5}\ \phi_{.}\ \gamma_{5}$	**2.22 ± 0.97**	**1.27 ± 0.54**
	S	Fall	2000	76	9	$p_{7}\ \phi_{7}\ \gamma_{.}$	2.04 ± 1.98	0.98 ± 0.89
Ruby-crowned Kinglet (*R. calendula*)	H	Fall	2000	595	38	$p_{5}\ \phi_{5}\ \gamma_{5}$	4.12 ± 6.42	2.28 ± 2.71
	H	Spring	1999	209	21	$p_{5}\ \phi_{.}\ \gamma_{5}$	2.04 ± 1.45	1.19 ± 1.05
	H	Spring	2000	198	29	$p_{.}\ \phi_{.}\ \gamma_{4}$	**1.82 ± 0.83**	0.96 ± 0.51
Gray-cheeked Thrush (*Catharus minimus*)	H	Fall	1999	118	27	$p_{6}\ \phi_{6}\ \gamma_{.}$	**13.66 ± 4.33**	**6.82 ± 2.33**
Swainson's Thrush (*C. ustulatus*)	H	Fall	2000	116	35	$p_{.}\ \phi_{7}\ \gamma_{.}$	3.34 ± 2.67	1.68 ± 1.35
Hermit Thrush (*C. guttatus*)	H	Fall	1999	165	27	$p_{7}\ \phi_{7}\ \gamma_{7}$	**5.14 ± 1.25**	**2.97 ± 0.82**
	H	Fall	2000	135	19	$p_{.}\ \phi_{.}\ \gamma_{6}$	**13.20 ± 3.45**	**9.35 ± 3.07**
Gray Catbird (*Dumetella carolinensis*)	H	Fall	2000	70	29	$p_{.}\ \phi_{7}\ \gamma_{.}$	**17.08 ± 7.81**	**7.15 ± 3.54**
Cedar Waxwing (*Bombycilla cedrorum*)	A	Fall	1998	87	31	$p_{7}\ \phi_{.}\ \gamma_{7}$	1.42 ± 0.85	0.77 ± 0.51
	A	Fall	2002	56	43	$p_{.}\ \phi_{.}\ \gamma_{7}$	4.95 ± 3.13	2.45 ± 1.44
	S	Fall	2000	76	42	$p_{7}\ \phi_{.}\ \gamma_{7}$	1.04 ± 0.70	0.54 ± 0.40
Northern Parula (*Parula americana*)	A	Spring	1998	58	21	$p_{7}\ \phi_{7}\ \gamma_{.}$	0.76 ± 0.62	0.38 ± 0.30

TABLE 2. Continued

Species	Site[a]	Season	Year	n	Stopover duration (days)	Chosen model	Total stopover duration estimate (days)[b]	Stopover-after estimate (days)[c]
Magnolia Warbler (*Dendroica magnolia*)	A	Spring	1997	237	35	$p_7\ \phi_7\ \gamma.$	1.58 ± 2.27	1.01 ± 2.05
	A	Spring	1998	561	33	$p.\ \phi_5\ \gamma_5$	**1.82 ± 0.58**	**1.02 ± 0.40**
	A	Spring	1999	265	28	$p_6\ \phi_6\ \gamma.$	2.23 ± 5.78	1.42 ± 5.19
	A	Spring	2001	358	39	$p_7\ \phi_7\ \gamma_7$	3.86 ± 7.76	1.76 ± 2.00
	H	Fall	2000	156	31	$p.\ \phi_5\ \gamma_5$	6.56 ± 3.66	3.27 ± 1.92
	H	Spring	2000	175	28	$p_7\ \phi_7\ \gamma_7$	1.78 ± 2.82	1.14 ± 2.37
	S	Spring	2000	159	30	$p_5\ \phi_5\ \gamma.$	2.00 ± 2.98	0.89 ± 0.75
Blackpoll Warbler (*D. striata*)	A	Fall	1996	78	32	$p_6\ \phi_6\ \gamma.$	**1.46 ± 0.50**	**0.73 ± 0.28**
	A	Fall	1998	120	32	$p.\ \phi_7\ \gamma.$	3.49 ± 2.89	1.77 ± 1.53
Black-and-white Warbler (*Mniotilta varia*)	A	Fall	1998	78	46	$p.\ \phi.\ \gamma_7$	**3.83 ± 1.54**	**1.99 ± 0.84**
American Redstart (*Setophaga ruticilla*)	A	Fall	1996	141	44	$p_7\ \phi_7\ \gamma_7$	2.72 ± 3.54	1.36 ± 0.74
	A	Fall	1997	142	41	$p.\ \phi.\ \gamma_5$	3.53 ± 2.19	**1.75 ± 0.81**
	A	Fall	1999	99	48	$p\ .\phi.\ \gamma_7$	4.67 ± 2.53	2.43 ± 1.38
	A	Fall	2000	210	40	$p_5\ \phi_5\ \gamma_5$	7.19 ± 14.75	5.01 ± 14.75
	A	Fall	2001	113	50	$p.\ \phi.\ \gamma_7$	3.59 ± 1.85	**1.78 ± 0.58**
	A	Fall	2002	144	47	$p_6\ \phi.\ \gamma_6$	**3.56 ± 1.33**	**1.94 ± 0.83**
	A	Spring	1997	103	29	$p.\ \phi_6\ \gamma.$	4.59 ± 3.69	3.02 ± 3.24
	A	Spring	1998	189	25	$p.\ \phi.\ \gamma_5$	**3.16 ± 0.63**	**1.79 ± 0.40**
	A	Spring	2000	143	34	$p_6\ \phi.\ \gamma_6$	3.65 ± 5.23	**1.46 ± 0.57**
Ovenbird (*Seiurus aurocapillus*)	A	Spring	1997	90	30	$p_6\ \phi_6\ \gamma_6$	6.27 ± 14.12	0.94 ± 1.02
Northern Waterthrush (*S. noveboracensis*)	A	Fall	1997	206	41	$p.\ \phi.\ \gamma_7$	5.24 ± 3.30	**2.55 ± 0.73**
	A	Fall	1999	153	46	$p.\ \phi.\ \gamma_7$	**7.49 ± 1.46**	**4.06 ± 0.90**
	A	Fall	2001	197	43	$p_7\ \phi_7\ \gamma.$	**8.86 ± 3.13**	**4.33 ± 2.09**
	A	Fall	2002	162	45	$p.\ \phi.\ \gamma_6$	7.89 ± 5.18	**3.97 ± 1.39**
	S	Fall	2000	100	43	$p.\ \phi.\ \gamma_7$	**3.06 ± 0.76**	**1.53 ± 0.39**
Wilson's Warbler (*Wilsonia pusilla*)	H	Fall	2000	50	25	$p.\ \phi_6\ \gamma_6$	3.27 ± 3.05	**1.32 ± 0.30**
	H	Spring	2000	100	23	$p_5\ \phi_5\ \gamma.$	**2.64 ± 0.69**	**1.35 ± 0.45**
White-throated Sparrow (*Zonotrichia albicollis*)	A	Spring	2002	247	28	$p_6\ \phi.\ \gamma_6$	3.15 ± 4.73	1.00 ± 0.52
	H	Fall	2000	539	35	$p_7\ \phi_7\ \gamma.$	**6.95 ± 2.75**	**3.47 ± 1.68**
	H	Spring	1999	126	21	$p_7\ \phi_7\ \gamma.$	0.93 ± 0.80	0.46 ± 0.39

[a] A = Appledore Island, Maine; H = Hamlin Beach State Park, New York; S = Star Island, New Hampshire.

[b] Mean ± SE of the total stopover estimate (following Schaub et al. 2001). Estimates in boldface had a CV of <50%. CV values were calculated as (SE/mean) × 100.

[c] Mean ± SE of the stopover-after estimate (using equation 5 in Efford 2005). Estimates in boldface had a CV of <50%. CV values were calculated as (SE/mean) × 100.

confidence level. It is worth noting that this simulation test has a Type I error rate of 5% (i.e., 5% chance of passing the GOF test when the model does not have adequate descriptive power); however, the expected Type II error rate (the chance that the model has failed GOF when, in fact, it has adequate descriptive power) is not known, so we cannot even say with certainty that the rate of GOF failure is greater than expected by chance. The contingency table GOF tests implemented in U-CARE also were severely limited by the sparseness of the data (only 42% of estimable capture histories could be tested using U-CARE).

For all capture histories used in this study, it was necessary to reduce the number of parameters in the fitted model from the number present in a fully time-dependent model to estimate all parameters successfully. Our results indicated that MDC intervals from 3 to 7 days were necessary to reduce the parameter count in the models sufficiently to estimate all parameters. Parameter reduction was necessary even for relatively large sample sizes (up to 595 specimens captured over 38 days). The only current alternative to the MDC method of reducing the number of parameters is pooling the data—with its attendant problems of possible parameter bias (Hargrove and Borland 1994, Morris et al. 2005b). If pooling is desirable in a given study, the MDC interval approach outlined here could be adapted to determine the minimum pooling interval necessary, based on parameter estimability. Regardless of the method, successful use of CMR models on banding data will often require some form of parameter reduction.

In our current work, the CV of total stopover duration measures the relative uncertainty in the derived parameter of interest. The CV includes both biological variability and variability due to parameter estimation uncertainty. Given our current available data, it is somewhat difficult to determine the extent of the biological contribution versus the sampling-related contribution. Again, long minimum stopover duration might indicate heterogeneity in the population. However, corresponding increases in (1) the fraction of capture histories with a CV of <50% and (2) the number of observations per parameter (Table 1) indicate some variation due to sample size. Overall, more estimates of stopover duration had a CV of <50% when using the stopover-after statistic (28 capture histories) than when using the total stopover statistic (23 capture histories). Thus, in addition to the theoretical points raised by Efford (2005), the statistic based on his equation 5 resulted in more useable estimates of stopover duration based on banding data.

Most of the capture histories that were estimable and had applicable models in this study were collected during fall migration (Table 2). Previous work on Appledore Island resulted in higher rates of recapture and documented longer minimum stopover durations during fall migration than in spring migration (Morris et al. 1994, Morris and Glasgow 2001); this may have helped increase the number of observations per parameter available in our study, which, in turn, may have resulted in higher estimability. We did not see a specific pattern related to avian biology that explained the pattern of capture histories with low CV values. Although most of the capture histories with low CV values were obtained during fall banding, this proportion was similar to the proportion of fall capture histories that had applicable models. The capture histories with low CV values represented a wide range of species (Table 2). Species that had low CV values over multiple seasons included those captured in high numbers, such as Red-eyed Vireo (*Vireo olivaceus*), American Redstart (*Setophaga ruticilla*), and Northern Waterthrush (*Seiurus noveboracensis*).

Our results document the difficulty associated with parameter estimability when using passerine banding data for capture-mark-recapture models of stopover duration. We are not implying that these methods cannot or should not be used on this type of data, but rather they should be used cautiously, particularly when sample sizes are small. Efford (2005) suggests using a constant ϕ model for populations with no consistent trend in ϕ, which would reduce problems with estimability. Researchers planning to use these methods in migration banding studies should attempt to maximize the number of captures and recaptures during sampling periods to increase the likelihood of parameter estimability.

ACKNOWLEDGMENTS

This research was funded, in part, by Canisius College faculty research funding to SRM and HDS, and

HHMI Research Assistantships to AML, DAL, and MSM. We are very grateful to the many people who assisted at the Appledore Island Migration Banding Station. R. W. Suomala (Star Island) and D. Bonter (Braddock Bay Bird Observatory) generously provided their banding data for use in our analyses. We also gratefully acknowledge the assistance of R. J. Morris and two anonymous referees, who provided valuable comments on this paper. This paper is contribution 12 of the Appledore Island Migration Banding Station and contribution 127 of the Shoals Marine Laboratory.

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The Wilson Journal of Ornithology 118(4):527–531, 2006

MAXIMUM DIVING DEPTH IN FLEDGING BLUE-FOOTED BOOBIES: SKILL DEVELOPMENT AND TRANSITION TO INDEPENDENCE

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ABSTRACT.—We evaluated maximum diving depth and time spent at the nest of fledging Blue-footed Boobies (*Sula nebouxii*) at Isla El Rancho, Sinaloa, in the Gulf of California, Mexico. Within three consecutive 10-day post-fledging intervals, maximum diving depth was highly variable, but was not affected by sex, weight, or body condition. During the first days of post-fledging flight, maximum diving depth increased rapidly. By the second week after first flight, the plunge-dives of juveniles were almost as deep as those of adults. Parental care and attachment to the nest lasted several additional weeks (up to 40 days after first flight). Although their diving capacity rapidly reached a level similar to that of the adults, it appeared that juvenile boobies took much longer in acquiring other foraging skills. *Received 1 August 2005, accepted 5 July 2006.*

The speed with which juvenile birds acquire foraging abilities has important implications for the evolution of life histories (Wheelwright and Templeton 2003). It has been hypothesized that parental care continues until young birds acquire mobility and foraging skills adequate for survival. Additional parental care improves the survival of the offspring, but decreases long-term survival of the parents (Burger 1980).

Juvenile birds face major challenges in learning how to identify foraging areas and developing foraging techniques as the period of parental care ends (Burger 1980, Wheelwright and Templeton 2003). The study of newly volant birds can help elucidate the process of such learning. However, this is complicated in the wild, as fledglings can move freely through the colony site. Most of the few studies on the subject have focused on passerines, which have a rather short transition to independence (Moreno 1984, Wheelwright and Templeton 2003). In seabirds, the development of foraging skills and its relationship to parental care are not well known (Yoda et al. 2004). We are aware of only one such seabird study (Brown Booby, *Sula leucogaster*), although the birds were raised by humans (Yoda et al. 2004), which could have interfered with social learning processes. Even less is known about possible intersexual differences in the acquisition of foraging skills (Wheelwright et al. 2003).

The Blue-footed Booby (*S. nebouxii*) is a sexually dimorphic seabird: females are larger than males at fledging (Drummond et al. 1991). Parental care continues for a 6-week, post-fledging period (Nelson 1978). During this period, young birds fly out to sea but return to their nests, where they continue receiving food from the parents. In this study, we determined the maximum diving depths (MDD) of wild fledgling Blue-footed Boobies to (1) examine the ontogeny of MDD and compare it with the diving depths achieved by adults, and (2) examine the relationship between the development of diving skills and sexually related size dimorphism.

METHODS

Field work was conducted at Isla El Rancho (25° 10′ N, 108° 23′ W), a sandy, 120-ha island in the south-central Gulf of California, Mexico, at the mouth of Bahía de Santa Maria–La Reforma—a large coastal lagoon. The colony studied was located on the northeastern part of the island among 4-m-high sand dunes. About 500 pairs of Blue-footed Boobies nested in an area of <1 ha, with a maximum density of 0.6 nests/m^2.

Between January and May 2004, we visited the island 12 times for periods of 5 days and monitored 100 nests and 108 chicks that we had marked with unique combinations of color bands. During each visit, we checked the nests daily, and weighed and measured (culmen, ulna, and tarsus) all banded chicks every other day. Sex was determined from the length

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of ulna at fledging (males = 191–207 mm; females = 213–233 mm; Drummond et al. 1991). Fledging (age at first flight) was inferred when a bird with complete juvenile plumage left its nest site and returned with clean feet (feet were covered with excrement before the first trip to sea). For most birds, we could estimate the exact age at fledging (estimates were ± 2 days in some cases).

From 20 April to 26 May, we estimated MDD by attaching a capillary tube (Tygon, 8 mm internal diameter; Burger and Wilson 1988) to the lower side of a booby's central rectrix. Tubes were recovered one day after application. A total of 99 capillary tubes produced usable data: 67 from fledglings (48 individuals, 15 of which provided data for more than one date), 17 from adult males, and 15 from adult females. In addition, we estimated the amount of time that young spent at their nests by monitoring 38 nests hourly during 14-hr diurnal periods.

We tested the data for normality and homocedasticity with Kolmogorov-Smirnov and Levene's tests, respectively, for every group to be compared. We used parametric procedures when both requirements were met. We grouped the MDD data for post-fledging juveniles into 5-day age intervals. We then conducted a Mann-Whitney U-test to compare the MDD attained by male and female fledglings for each 5-day period.

We used a mixed-model ANOVA-ANCOVA for comparing 5-day periods (normality: $D = 0.17$–0.39; homocedasticity: $F_{4,39} = 0.98$, $P = 0.42$) to evaluate the possible effects of ontogeny on MDD. The number of days since first fledging was included as a covariate, with the 5-day periods as the fixed factor. Multiple flights of the same bird in 10-day intervals (1–10, 11–20, and ≥21 days after fledging) were compared with t-tests for dependent samples.

We found no significant differences between adult male and female MDD (3.4 ± 2.1 m and 3.6 ± 1.6 m, $n_1 = 15$ and $n_2 = 17$, respectively; $t = 0.33$, $P = 0.73$; normality: $D = 0.22$ and 0.23, respectively; homocedasticity: $F_{1,31} = 1.7$, $P = 0.26$). Therefore, we pooled the MDD of both sexes to compare adult MDD with that of juveniles that had fledged at least 15 days previously. We tested for age-related differences in MDD using a t-test (normality: $D = 0.19$ and 0.13, respectively; homocedasticity: $F_{1,49} = 3.96$, $P = 0.55$).

We used linear regressions to assess whether MDD might be a function of weight or body condition. Residuals from the regression of weight on culmen length were used as a body condition index. Using residuals of a regression between weight and body measurements as an index of condition is adequate when measurement errors and variations in body size are low (Schulte-Hostedde et al. 2005); the major assumption to be met is that the relationship between variables is linear, which was the case in our study ($r^2 = 0.73$, $P < 0.001$). To explore the relationship between days since first flight and time spent at the nest, we used a mixed ANOVA-ANCOVA model, with gender serving as the fixed factor and days since fledging included as a covariate. All statistical tests were considered significant at $\alpha = 0.05$, and reported values are means ± SD.

RESULTS

Female Blue-footed Booby chicks reached their maximum pre-fledging weight (2,071 ± 125.2 g) between 60 and 75 days of age, while males reached it (1,628 ± 117.5 g) between 60 and 70 days of age. Females were significantly heavier than males ($t_{49,54} = 18.43$, $P < 0.001$). After reaching their maximum weight, female chicks lost 8.5% of their weight and weighed 1,830 g ± 72.2 at first flight, whereas males lost 7% and weighed 1,470 g ± 63.5. Males began to fly earlier than females (83.4 ± 2.64 and 87.9 ± 3.8 days of age, $n_1 = 23$, $n_2 = 19$, respectively; $U = 67$, $P < 0.001$). MDD within any given period was highly variable (Fig. 1), and there were no statistical differences between male and female fledglings (1–5 days after first flight: $n_1 = 9$, $n_2 = 6$, $U = 19$, $P = 0.34$; 6–10 days: $n_1 = 6$, $n_2 = 9$, $U = 16$, $P = 0.38$; 11–15 days: $n_1 = 7$, $n_2 = 9$, $U = 25.5$, $P = 0.52$; 16–20 days: $n_1 = 4$, $n_2 = 6$, $U = 11$, $P = 0.83$).

We did not detect an effect of date on MDD, per se ($F_{1,38} = 3.31$, $P = 0.10$), but despite great within-interval variability, MDD increased with time since first flight throughout the first 15 days of flight (0–5 days = 1.68 ± 0.66 m, 6–10 days = 2.69 ± 0.81 m, 11–15 days = 3.02 ± 0.53 m; $F_{4,39} = 3.64$, $P = 0.012$; Fig. 1). By 16–20 days (3.11 ± 0.76

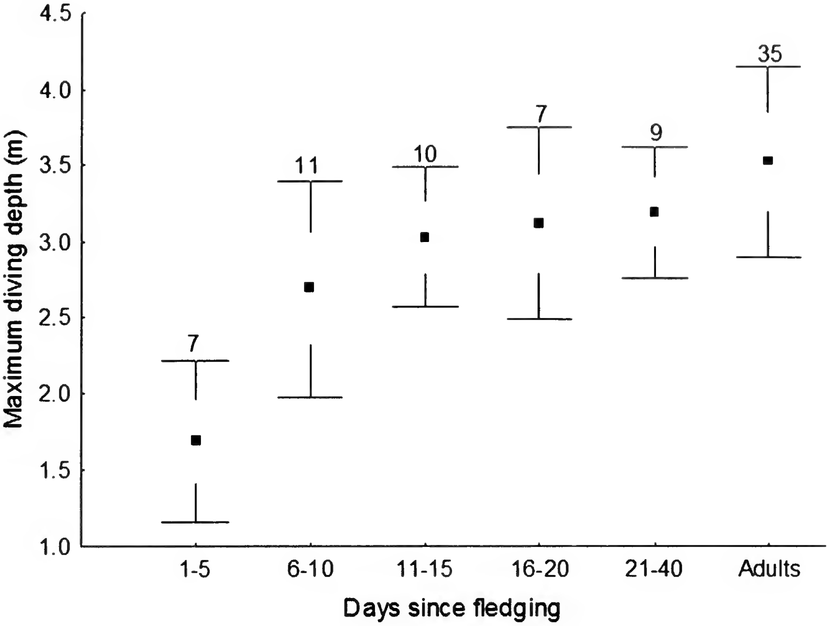

FIG. 1. Maximum diving depth of Blue-footed Boobies increased rapidly during the first 15 days after their first flight at Isla El Rancho, Sinaloa, Mexico, 2004. Fledglings then dived almost as deep as adults. Means ± SE (white zone) and 95% confidence intervals (whiskers) are shown. Sample size is indicated above whiskers.

m) and 21–40 days (3.18 ± 0.55 m; Fig. 1) since flight, MDD stabilized. The 15 juveniles for which we had >1 MDD value (there were 2 values for 9 birds and >2 for 6 birds) exhibited a similar tendency: during the first 10 days after fledging, dives were shallower than they were during the 11–20 day interval (1–10 days = 2.12 ± 0.70 m and 11–20 days = 3.03 ± 0.90 m, $t_{12} = -2.44$, $P = 0.032$). Birds for which we had >2 records made shallower dives during the first 10 days after fledging than they did ≥21 days post-fledging (1–10 days = 1.94 ± 0.35 m and ≥21 days = 3.42 ± 0.69 m, $t_4 = -5.05$, $P = 0.007$); there were no significant differences between the two later periods (11–20 days = 2.64 ± 0.71 m and ≥21 days = 2.90 ± 0.96 m, $t_7 = -0.51$, $P = 0.62$).

MDD of juveniles that had flown for at least 15 days did not differ from that of adult birds (2.99 ± 0.75 m and 3.51 ± 1.88 m, respectively, $t_{54} = -1.27$, $P = 0.26$). Weight was not correlated with diving depth within sex (males: $P = 0.71$; females: $P = 0.90$). The regression between MDD and body condition also was not significant ($P = 0.23$).

Juvenile birds progressively reduced their time at the nest after their first flight ($r^2 = 0.33$, $P < 0.001$), with no differences between males and females ($F_{1,29} = 0.11$, $P = 0.73$). After 25 days of flight, some individuals left the nest for at least the entire daylight period. Other young birds remained at their nests for >40 days (Fig. 2).

DISCUSSION

Blue-footed Booby parents reduce their provisioning to offspring just before the nestlings take their first flights (*sensu* Nelson 1978; JAC-G unpubl. data). This reduction may stimulate fledging and encourage the fledglings to develop foraging skills away from their nest. Juveniles make their first plunge dives on their first day of flight (every recovered capillary tube showed evidence of immersion, including four that were attached to birds just prior to their first flight).

Clearly, 15 days of learning were enough for juveniles to dive almost as deep as adults. Based on our observations, the fledglings made their first plunges at low angles and from low heights. As the days passed, the birds increased the plunge height and dives became more vertical. During the first days

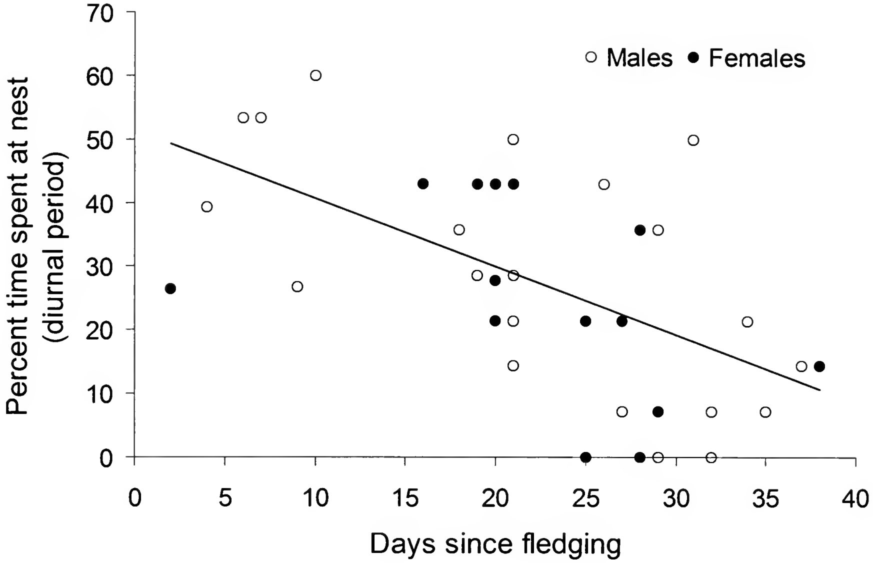

FIG. 2. The percent of diurnal time fledgling Blue-footed Boobies spent at the nest decreased with time since their first flight ($r^2 = 0.33$, $P < 0.001$) at Isla El Rancho, Sinaloa, México, 2004. This relationship is described by the equation $t_n = 0.5147 - 0.107 \times$ days since fledging, where t_n = percentage of diurnal time at nest.

after initiation of flight, fledglings also tended to fly in groups around the island, suggesting that social interactions might facilitate their development of diving and, perhaps, foraging skills.

For several weeks after their first flight, fledglings continued begging for food from their parents. Juveniles of other species usually cease begging when foraging for themselves becomes more profitable (Moreno 1984, Heinsohn 1991, Wheelwright and Templeton 2003); thus, the young birds in our study apparently required several additional weeks to become adequate foragers. Similar to other sulids (Burger 1980, Yoda et al. 2004), the Blue-footed Boobies at El Rancho exhibited gradual separation from their parents. Based on our observations, we hypothesize that there are two periods in the development of foraging skills: (1) an initial rapid improvement in the depth attained during plunge-dives, followed by (2) improvement in other behaviors, such as locating and capturing prey. Presumably, once birds begin catching fish, begging frequency and presence at the nest decrease. Some juveniles apparently achieved this level of independence at 25 days after fledging, while others required >40 days to do so.

It is unlikely that temporal changes in the depth at which prey were found affected our recorded MDD in fledglings. Our data did not exhibit any effects of date, and fledglings did not exhibit much synchrony in dates of first flight that could confound our data. Some fledglings were already independent by the time others began to fly and, in some cases, >2 months had passed between early- and late-fledging birds. We did not find evidence of temporal patterns in adult MDDs.

Despite the Blue-footed Booby's distinct sexual dimorphism in size and gender-influenced differences in growth and date of first flight (Torres and Drummond 1999; this study), we found no gender differences in MDD. Given the limitations of capillary tubes, however, further study of the relationship between sexual dimorphism in size and booby diving performance is warranted. It seems that fledging Blue-footed Boobies develop plunge-diving skills and attain MDDs similar to those of adults relatively quickly. However, this does not imply that juvenile feeding success and/or foraging performance is equivalent to that of adults. Their nest attendance and insistent begging for long periods indicate that foraging for themselves, along with developing prey-finding and prey-capturing skills, delays the full independence of young Blue-footed Boobies.

ACKNOWLEDGMENTS

We are grateful to CONACYT and SEMARNAT for funding. A. Aguilar, and the M. A. Gonzalez-Bernal family provided logistical support. M. Prado and E. A. Peñaloza assisted during field work. J. Awkerman provided editorial advice. S. Herzka, E. A. Schreiber, D. J. Anderson, and an anonymous reviewer greatly improved this manuscript; we are grateful to all of them.

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The Wilson Journal of Ornithology 118(4):532–536, 2006

VEGETATIVE AND THERMAL ASPECTS OF ROOST-SITE SELECTION IN URBAN YELLOW-BILLED MAGPIES

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ABSTRACT.—We examined vegetative and thermal aspects of roost-site selection in urban Yellow-billed Magpies (*Pica nuttalli*) in Sacramento, California, from winter 2003 to spring 2004. Vegetation used for roosting included cultivated species such as glossy privet (*Ligustrum lucidum*), English ivy (*Hedera helix*), and white mulberry (*Morus alba*), and native species such as interior live oak (*Quercus wislizeni*), valley oak (*Q. lobata*), and California laurel (*Umbellularia californica*). Percent canopy cover was consistently high (mean = 94% ± 1.9 SD). Mean roost height was 9.7 m ± 3.5 SD and the mean height at which magpies roosted was 6.6 m ± 2.0 SD. Communal roosts were generally located within or near riparian corridors. Magpies roosted in relatively warm microhabitats, but they did not appear to obtain a thermal advantage by roosting communally. The timing of roost occupancy was restricted primarily to times when the roost was thermally advantageous. *Received 22 August 2005, accepted 2 May 2006.*

The Yellow-billed Magpie (*Pica nuttalli*) is found chiefly in the Central Valley and lower foothills of California and is relatively abundant in the residential areas of Sacramento (Reynolds 1995). The roosting behavior of this species is not well documented, especially regarding urban populations. However, rural magpies studied at and near Hastings Natural History Reserve (HNHR) in Monterey County, California, roost almost exclusively in live oaks (*Quercus* spp.; Verbeek 1973), where roost size may exceed several hundred birds (Birkhead 1991).

The evolution of communal roosting has been attributed to several factors, including a decrease in predation risk (Pulliam 1973), an increase in foraging efficiency (Marzluff et al. 1996), and a reduction in thermoregulation demands (Francis 1976). The thermoregulatory requirements of magpies are greatest during the winter months (Mugaas and King 1981), indicating that roost-site selection is important to energy conservation in winter. By roosting in dense vegetation or cavities, birds can reduce heat loss and gain protection from wind and rain (Walsberg 1986). Roosting over water or moist soil also may moderate extreme temperatures (Møller 1985). Timing of roost occupancy is also critical to energy conservation: Black-billed Magpies (*Pica hudsonia*) are known to spend relatively more time at the roost when faced with cold temperatures (Reebs 1986).

Our goal was to document vegetative and thermal aspects of roost-site selection in Yellow-billed Magpies inhabiting urban sites. We hypothesized that urban Yellow-billed Magpies (1) roost in a greater number of plant species than magpies in rural settings; (2) select roost sites that provide thermal advantages such as high percent canopy cover, and proximity to water and other places where temperatures may be moderated by nearby substrates; (3) may, when roosting in large groups, increase the temperature of the roost via collective production of body heat; and (4) occupy the roost only when its temperature is higher than that of the surrounding habitat.

METHODS

We located eight Yellow-billed Magpie communal roosts in the urban (residential) areas of Sacramento, California (Fig. 1, Table 1), by following magpies from their foraging grounds to their roost sites and by querying the local ornithological community. Data collection took place from December 2003 through May 2004. We visited each roost once per week during morning roost departures or evening roost arrivals to ascertain roost occupancy and determine where the birds slept. During each observation, we recorded the number of birds arriving at, or departing from,

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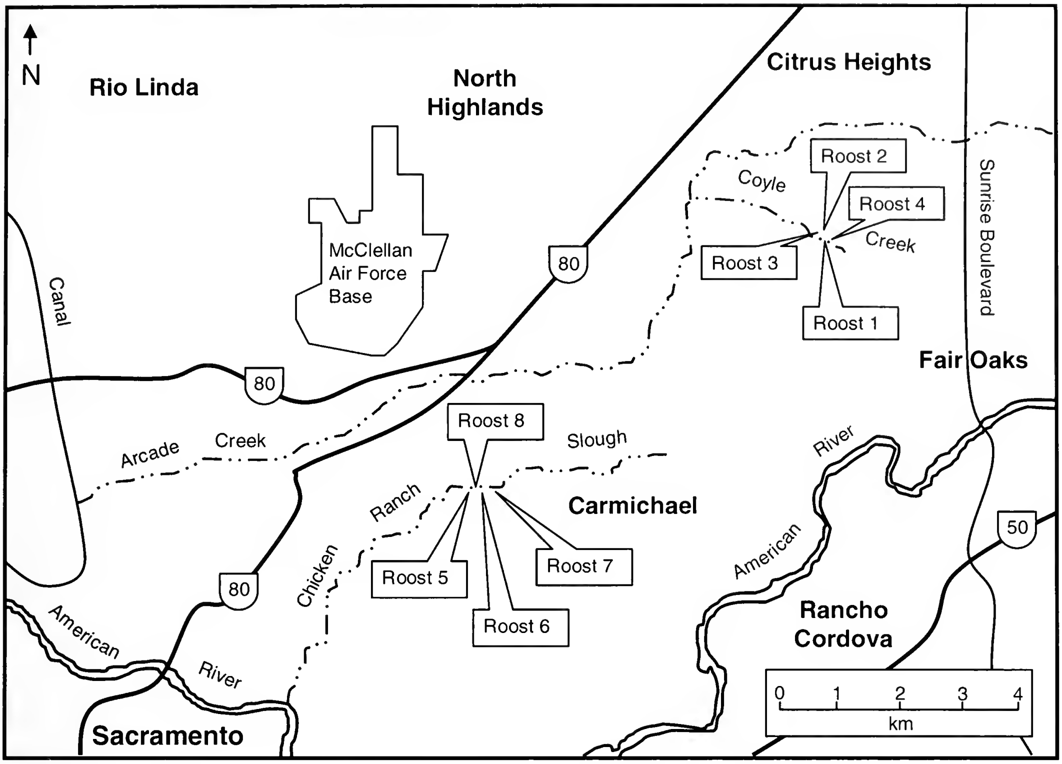

FIG. 1. Study area and locations of Yellow-billed Magpie roosts in Sacramento, California, winter 2003 through spring 2004.

the roost per min for the entire period of roost entry or exodus. On average, morning observation periods lasted 75 min and evening observation periods lasted 95 min. Occasionally we made nighttime visits with flashlights to confirm where birds roosted (the birds were slightly wary, but very tolerant, of this activity).

We used a densiometer to determine the mean percent canopy cover of roosts and a clinometer to determine mean height of all trees/shrubs comprising each roost (roost height) and mean height of each group of magpies perched in their roosts. All canopy cover measurements were made in the last 2 weeks of May to ensure that our estimates were comparable across all roosts. We measured the distance from each roost center to the closest water body (always a creek) by using a Garmin eTrex Legend Global Positioning System (Olathe, Kansas).

From 7 December 2003 through 13 February 2004, we recorded roost temperatures with Hobo data-logging thermometers (Onset Computer Corporation, Bourne, Massachusetts). We collected paired samples at 20 points within two known roosts and at 20 points within eight potential roosts (unoccupied vegetation) that were located within a 200-m radius of a known roost. Potential roosts were selected according to their similarity to known roosts in terms of tree or shrub

TABLE 1. Latitude and longitude coordinates of urban Yellow-billed Magpie communal roost sites in Sacramento, California, 2003–2004.

Roost no.	Latitude	Longitude
1	N 38° 40.021′	W 121° 18.221′
2	N 38° 40.081′	W 121° 18.241′
3	N 38° 40.051′	W 121° 18.262′
4	N 38° 40.043′	W 121° 18.207′
5	N 38° 37.324′	W 121° 22.760′
6	N 38° 37.278′	W 121° 22.666′
7	N 38° 37.278′	W 121° 22.640′
8	N 38° 37.328′	W 121° 22.696′

TABLE 2. Characteristics of urban communal roosts of Yellow-billed Magpies in Sacramento, California, 2004.

Roost no.	Mean canopy cover (%)	Mean height of vegetation used (m)	Mean height of magpie perches (m)	Distance to water (m)	Estimated maximum no. magpies
1	92.2 (*n* = 6)	11.2 (*n* = 6)	7.5 (*n* = 6)	0	879
2	95.9 (*n* = 19)	8.5 (*n* = 19)	5.4 (*n* = 19)	106	133
3	93.5 (*n* = 1)	7.9 (*n* = 1)	6.5 (*n* = 1)	62	14
4	91.0 (*n* = 1)	17.6 (*n* = 1)	11.0 (*n* = 1)	29	8
5	94.5 (*n* = 18)	9.2 (*n* = 18)	6.2 (*n* = 18)	56	818
6	95.8 (*n* = 2)	8.6 (*n* = 2)	6.0 (*n* = 2)	89	27
7	91.7 (*n* = 1)	8.9 (*n* = 1)	5.9 (*n* = 1)	56	12
8	94.8 (*n* = 3)	5.7 (*n* = 3)	4.2 (*n* = 3)	13	7
Mean	93.7	9.7	6.6	51	237
SD	1.9	3.5	2.0	36	380

species height, percent canopy cover, and proximity to water. Within a given roost, we used a random number generator to select a compass bearing, distance, and height for locating the tree or shrub in which we would place the data-loggers. For each of the paired temperatures, data-loggers were placed at similar heights within the range of heights at which magpies roosted in the area. Data-loggers were taped to the upper end of a 2-m-long stick, at the top of which we attached a bent coat hanger that allowed us to hang the data-loggers on lateral branches between the tree or shrub center and the outer perimeter of the canopy (where magpies roosted). All paired recordings took place at 05:00 PST. Using SPSS (1998), we conducted a one-tailed, paired-sample *t*-test ($\alpha = 0.05$; see Zar 1999) to determine whether the roost microhabitat was significantly warmer than the nearby potential roost microhabitat.

To determine whether any temperature difference in occupied versus unoccupied roosts was due to the birds' presence, we recorded temperatures at 45-min intervals in two randomly selected locations: one within a known roost site (Roost 1) and another in an area of unoccupied vegetation within 200 m of Roost 1. We recorded temperatures at these two sites on two occasions: once on a night when the known roost was occupied (by 317 individuals) and again a week later (the data-loggers were left in place) when the known roost was temporarily unoccupied (temporary roost abandonment was a normal phenomenon related to the birds' seasonal movements). On the evening Roost 1 was occupied, we recorded the time at which magpies arrived and subsequently departed the following morning to determine whether the timing of roost occupancy is limited to when the roost is warmer than its surroundings.

RESULTS

A total of 18 plant species were used for roosting. Species native to California included (in approximate relative order of usage) interior live oak (*Quercus wislizeni*), valley oak (*Q. lobata*), California laurel (*Umbellularia californica*), boxelder (*Acer negundo*), bishop pine (*Pinus muricata*) and MacNab's cypress (*Cupressus macnabiana*). Species not native to California included glossy privet (*Ligustrum lucidum*), English ivy (*Hedera helix*) that had overtaken trees, an undetermined species (no floral structures were present) of bamboo (Bambusoideae), white mulberry (*Morus alba*), Japanese cheesewood (*Pittosporum tobira*), Chinese photinia (*Photinia serrulata*), dense logwood (*Xylosma congestum*), oleander (*Nerium oleander*), Chinese elm (*Ulmus parvifolia*), cherry laurel (*Prunus laurocerasus*), pomegranate (*Punica granatum*), and southern magnolia (*Magnolia grandiflora*). Deciduous species were only occupied when leafed out. Canopy cover at roosts, comprising leaves and dense networks of branches, was consistently high (>90%; Table 2). The height of occupied vegetation varied; however, magpies always roosted in the upper third of the vegetation. All roosts were located near a creek and Roost 1 was situated almost entirely over a creek.

The microhabitat of known roosts was sig-

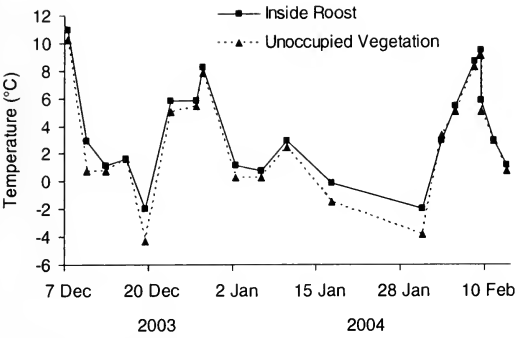

FIG. 2. Morning (05:00 PST) temperatures recorded in urban communal roosts of Yellow-billed Magpies and in nearby potential roost sites (unoccupied vegetation), December 2003 through February 2004, Sacramento, California.

nificantly warmer than that of nearby potential roosts (mean difference = 0.72° C ± 0.72, range = 0.40–0.88° C, $P < 0.001$; Fig. 2). The 45-min interval sampling showed that, just after the birds' median arrival time, known roost temperature exceeded potential roost temperature (Fig. 3A). About 25 minutes before the magpies left on the following morning, temperature in the known roost dropped below that of the potential roost. The same temperature inversion occurred a week later when the known roost was temporarily unoccupied (Fig. 3B), but the mean temperature difference was greater when the roost was unoccupied (0.65° C ± 0.23 when occupied; 1.54° C ± 0.41 when unoccupied).

DISCUSSION

In contrast to rural magpies roosting at and near HNHR, urban magpies in our study roosted in a variety of plant species. This difference is undoubtedly due to the greater diversity of plant species in the urban setting that provides the characteristics necessary for suitable roost sites. However, both rural and urban populations of the Yellow-billed Magpie appear to roost only in dense evergreen vegetation during winter; in contrast, some Black-billed Magpie and Common Magpie (*Pica pica*) populations roost in deciduous vegetation for part or all of the winter (Møller 1985, Reebs 1987). Avoiding wind exposure has been identified as one of the most important factors in roost-site selection (Walsberg 1986), and magpies can reduce their metabolic demand substantially by roosting in dense vegetation during winter (Mugaas and King 1981). Magpies may also deter predation events by roosting in dense vegetation. Cooper's (*Accipiter cooperii*) and Red-shouldered (*Buteo lineatus*) hawks occasionally prey upon magpies as the magpies depart from their roosts (Crosbie 2004).

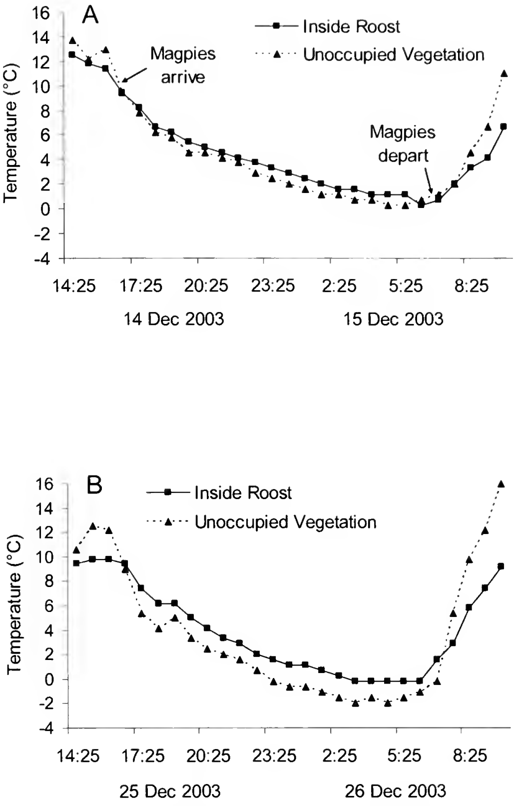

FIG. 3. Temperatures recorded at 45-min intervals in (A) an urban communal roost occupied by 317 Yellow-billed Magpies and in nearby unoccupied vegetation (an interior live oak) during the night of 14–15 December 2003, Sacramento, California, and (B) in a temporarily unoccupied urban communal roost of the Yellow-billed Magpie and in nearby unoccupied vegetation (an interior live oak) during the night of 25–26 December 2003, Sacramento, California.

Whereas magpies at and near HNHR roost at heights ≥10–20 m (Reynolds 1995), roosting height in this study was lower; this was probably due, in part, to the fact that there was no taller vegetation that provided dense cover. Similar to magpies studied in Denmark (Møller 1985) and Canada (Reebs 1987), magpies in this study roosted near water, likely due to the moderating effect that water or moist soil may have on nighttime temperatures (Møller 1985).

Wintering blackbirds studied by Francis (1976) roosted in microhabitats that were 1.0 to 1.5° C warmer than their surroundings, slightly greater than the range of difference observed in this study. However, the control site used by Francis (1976) was in a clearing rather than in vertical vegetation, as was the case in our study. The temperature difference between magpie roosts and nearby potential roost sites was greatest on the coldest nights (Fig. 2), indicating that roosts are especially favorable during cold spells. Similarly, magpies in Teruel, Spain, prefer thermally advantageous roosts when temperatures are low (Miranda and Gonzalez 2000). In our study, the timing of roost arrival and departure conformed almost precisely to the times at which the temperature of the roost became warmer or cooler, respectively, than the surrounding habitat (Fig. 3A). However, these birds may not gain any thermoregulatory benefit by roosting together: the temperature difference between the roost and nearby unoccupied vegetation was not greater when the roost was occupied than when unoccupied (Fig. 3).

In conclusion, urban-dwelling Yellow-billed Magpies roosted in a variety of plant species. Roost-site selection was biased toward habitat structure that provided thermal advantages, such as a high percent of overhead cover, proximity to water, and warm temperatures relative to surrounding habitat. It does not appear that magpies gain any thermal benefit via collective body heat production, but the timing of roost occupancy in winter is limited primarily to times when the roost is thermally advantageous. The habit of roosting near water may be detrimental due to the recent arrival of West Nile virus. Further study on roost-site selection, mosquito presence, and management options, where necessary, is warranted.

ACKNOWLEDGMENTS

This paper is based on part of a thesis presented to the Department of Biological Sciences at California State University, Sacramento, by Scott P. Crosbie, in partial fulfillment of the requirements for the degree of Master of Science. We thank W. E. Avery, M. F. Baad, L. R. Crosbie, M. D. Reynolds, H. B. Ernest, and three anonymous referees for their support, guidance, and review of this manuscript. We are grateful to all property owners who allowed us access to roosts, especially W. D. Shepard, M. Schlenker, and M. Morris. We also thank the California State University Sacramento Foundation for a monetary award to purchase equipment used in this study.

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The Wilson Journal of Ornithology 118(4):537–546, 2006

NESTING SUCCESS OF GRASSLAND AND SAVANNA BIRDS ON RECLAIMED SURFACE COAL MINES OF THE MIDWESTERN UNITED STATES

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ABSTRACT.—Reclaimed surface coal mines in southwestern Indiana support many grassland and shrub/savanna bird species of conservation concern. We examined the nesting success of birds on these reclaimed mines to assess whether such "unnatural" places represent productive breeding habitats for such species. We established eight study sites on two large, grassland-dominated mines in southwestern Indiana and classified them into three categories (open grassland, shrub/savanna, and a mixture of grassland and shrub/savanna) based on broad vegetation and landscape characteristics. During the 1999 and 2000 breeding seasons, we found and monitored 911 nests of 31 species. Daily nest survival for the most commonly monitored grassland species ranged from 0.903 (Dickcissel, *Spiza americana*) to 0.961 (Grasshopper Sparrow, *Ammodramus savannarum*). Daily survival estimates for the dominant shrub/savanna nesting species ranged from 0.932 (Brown Thrasher, *Toxostoma rufum*) to 0.982 (Willow Flycatcher, *Empidonax traillii*). Vegetation and landscape effects on nesting success were minimal, and only Eastern Meadowlarks (*Sturnella magna*) showed a clear time-of-season effect, with greater nesting success in the first half of the breeding season. Rates of Brown-headed Cowbird (*Molothrus ater*) parasitism were only 2.1% for grassland species and 12.0% for shrub/savanna species. The nesting success of birds on reclaimed mine sites was comparable to that in other habitats, indicating that reclaimed habitats on surface mines do not necessarily represent reproductive traps for birds. *Received 1 August 2005, accepted 10 April 2006.*

Several bird species have benefited in recent decades from the reclamation of surface coal mines in the midwestern United States (Bajema et al. 2001, DeVault et al. 2002, Ingold 2002). The Surface Mining Reclamation Act of 1977 and earlier laws led (perhaps unintentionally) to mine reclamation techniques that favored the production of grasslands rather than forested habitats (Brothers 1990), resulting in hundreds of km^2 of newly created grasslands. These "mine grasslands" harbor a diverse assemblage of grassland birds, many of which are of management concern at state and federal levels. Recent studies in southwestern Indiana, covering 19 reclaimed mines, suggest that populations of key grassland bird species, such as Grasshopper (*Ammodramus savannarum*) and Henslow's (*A. henslowii*) sparrows, are quite large (Bajema et al. 2001, DeVault et al. 2002). Reclaimed mines also contain scattered trees (from plantings and natural succession) that approximate the structure of savanna habitat to a substantial degree (Scott et al. 2002, Scott and Lima 2004). Accordingly, these reclaimed mines harbor several savanna bird species (DeVault et al. 2002) of conservation concern (Davis et al. 2000, Hunter et al. 2001).

The size of reclaimed mines in the midwestern United States is one of their most important characteristics—several exceed 2,000 ha (Bajema and Lima 2001, Ingold 2002). Many grassland bird species appear to be "area sensitive" in that usually they are found only in grassland fragments of a given size or greater (Herkert 1994, Walk and Warner 1999, Winter and Faaborg 1999; but see Horn et al. 2000, Johnson and Igl 2001). Most studies suggest that grasslands >50–100 ha should contain a full complement of grassland passerines. Virtually all grasslands on reclaimed mines in southwestern Indiana are >100 ha (Bajema and Lima 2001). Furthermore, small grassland size may be associated with poor nesting success, reflecting the close proximity of habitat edge, which can lead to greater predator densities (Winter et al. 2000, Herkert et al. 2003) and greater rates of Brown-headed Cowbird (*Molothrus ater*) parasitism (Johnson

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and Temple 1990). These effects of habitat size are similar to those documented for many forest-nesting passerines (e.g., Donovan et al. 1995, Robinson et al. 1995).

Even though large reclaimed coal mines in the Midwest harbor a variety of breeding bird species, they are decidedly unnatural places in terms of vegetation (Scott and Lima 2004). Hence, it is conceivable that reclaimed mines function as giant ecological "traps" that divert breeding birds away from more productive habitats (*sensu* Gates and Gysel 1978). Even though grassland birds can breed successfully in non-native grasslands (e.g., Warner 1994, Best et al. 1997, Kershner and Bollinger 1998, Robb et al. 1998, Ingold 2002, Monroe and Ritchison 2005), the possibility that they represent ecological traps is not trivial. For example, reclaimed midwestern mines often are dominated by tall fescue (*Festuca arundinacea*; Scott et al. 2002, Scott and Lima 2004), which often is infected with a symbiotic fungal endophyte (*Neotyphodium coenophialum*). Such infected fescue is associated with declines in plant diversity and lowered reproductive success of herbivores (vertebrate and invertebrate; Clay and Holah 1999). Tall fescue might reduce insect production and render reclaimed mine grasslands into poor breeding habitat. Although tall fescue also may affect the breeding prospects of savanna bird species, they might be less affected than their grassland counterparts.

There are few data available for assessing whether birds inhabiting reclaimed surface mines are nesting successfully. Thus, our goal in this study was to investigate patterns of avian nesting success within reclaimed surface coal mines, with the larger goal of evaluating whether reclaimed mines provide productive breeding habitats for grassland and savanna birds.

METHODS

Study sites.—Our work spanned the 1999 and 2000 breeding seasons. In both years, field work began in late April and continued through the 1st week of August. Study sites were established at two large reclaimed surface coal mines in west-central Indiana within 30 km of the city of Terre Haute. Four sites were established at the Chinook Mine (39° 28′ N, 87° 13′ W; 2,000 ha) in Clay and Vigo counties and four were established at the Universal Mine (39° 36′ N, 87° 28′ W; 3,450 ha) in southern Vermillion County. The Chinook sites ranged in size from 39 to 67 ha, whereas the Universal sites were smaller (12 to 38 ha) due to constraints imposed by cattle and haying operations. Chinook Mine comprised 61% undisturbed grassland and 18% hayfields; the remaining 21% comprised relatively even percentages of wetlands, row crops, and forests (Bajema and Lima 2001). Universal Mine was 33% undisturbed grassland and 43% hayfields and cattle pastures, with the remaining 24% split about evenly between forest and lakes/wetlands (Bajema and Lima 2001).

Study sites were chosen to represent the range of grassland-dominated habitats found in the reclaimed surface coal mines of southwestern Indiana. Two study sites (one in each mine) were classified as "open grassland." We defined open grassland sites as relatively undisturbed areas (no mowing for ≥ 2 years, usually many more) that were dominated by grasses ($>95\%$, by area), with some forbs and very few saplings, trees, or shrubs (Scott et al. 2002). Open grasslands represented the most abundant habitat type found on most reclaimed surface mines (Bajema and Lima 2001). Nests found in these open sites were, on average, 760 m from the nearest mature forest habitat, with many nests well over 1,000 m from forest.

Three study areas were classified as "shrub/savanna" sites (one at Chinook Mine and two at Universal Mine). We defined shrub/savanna sites as predominantly grassy habitats with many scattered young trees (4–8 m high, generally open canopy) and shrubs, often representing a transition zone between grassland and forested areas. Small groves of trees also were associated with small wetland areas. Black locusts (*Robinia pseudoacacia*) dominated in shrub/savanna sites, although significant numbers of oaks (*Quercus* spp.), eastern cottonwoods (*Populus deltoides*), and mature autumn olives (*Elaeagnus umbellata*) were found in some areas. "Shrubby" species included young saplings of these tree species, along with hawthorn (*Crataegus* spp.) and multiflora rose bushes (*Rosa multiflora*). Shrub/savanna sites were adjacent to mature forest (and hence were mainly on the edges of the reclaimed mines). The average distance between nests found on shrub/savanna sites and the forest edge was 240 m. Shrub/savanna sites contained significant (30–60%, by area) open grassland habitat.

Finally, we designated the remaining three study sites (two at Chinook Mine and one at Universal Mine) as "mixed" sites. Mixed sites were defined as mostly open grassland habitat with a few areas of significant shrub/savanna habitat. In general, these sites were 70–80% open grassland. The average distance between nests found on mixed sites and the nearest mature forest habitat was 430 m.

Nest location and monitoring.—Nest searches were conducted daily in 1999 and 2000 from early morning until early afternoon by a team of three to five field workers. Nests were detected by (1) rope dragging, (2) following adults that were carrying food and nesting material, and (3) systematic searches of likely nesting sites (Martin and Geupel 1993). During the 2000 field season, we also used a thermographic imager to aid in nest detection (Galligan et al. 2003).

When a nest was located, a small colored flag was placed 10 m to the north of it and a small piece of colored tape was tied to vegetation 5 m south of the nest (Picozzi 1975, Walk 2001). The accurate alignment of flag, tape, and nest allowed workers to relocate nests quickly with minimal disturbance. Species associated with each nest were identified, and nests were checked only every 3 to 4 days to minimize disturbance (Bart 1977). During each nest check, we recorded the presence or absence of adults, the number of eggs or chicks, and, if appropriate, the developmental stage of the chicks. We also recorded indicators of nestling mortality or cowbird parasitism.

Vegetation and landscape variables.—We gathered basic information on the physical relationships between nests, the surrounding vegetation, and major landscape features; however, we limited analyses of these variables to grassland bird species, whose nests were located in greater numbers than savanna species. For each nest, we recorded height above ground, species and height of the vegetation in which it was placed, dominant vegetation and vegetation height within 1 m of the nest, litter depth at the nest, percent cover of litter within 1 m of the nest, distance to the nearest forest edge, and distance to the nearest tree (>1 m high). We used GPS units to record the location of all nests and to delineate nearby forested areas.

Data analyses.—We estimated the daily probability of nest survival (DNS) for each species according to the Mayfield method (Mayfield 1961, 1975). We assumed that any relevant nesting event (e.g., hatching, failure, fledging) occurred at the midpoint of the interval between nest visits. A nest was considered successful when it fledged one or more young (Mayfield 1961, 1975).

Our analyses were limited primarily to univariate tests of vegetation, landscape, and temporal variable effects on DNS or the fate of individual nests (success or failure). We tested for interactions only for study site and time of season. We compared DNS estimates across categorical variables (i.e., among years, sites, and different habitat types) by using CONTRAST (Hines and Sauer 1989). CONTRAST uses a generalized χ^2 statistic that allows multiple comparisons of survival rates from different time periods or study areas (Sauer and Williams 1989). We compared DNS among years and sites for all species listed in Table 1. Because we found large numbers of Field Sparrow (*Spizella pusilla*), *Ammodramus* spp. (Henslow's and Grasshopper sparrows, combined), Dickcissel (*Spiza americana*), Red-winged Blackbird (*Agelaius phoeniceus*), and Eastern Meadowlark (*Sturnella magna*) nests, we were able to examine DNS trends within breeding seasons (comparing DNS between the first and second halves of the breeding seasons) and between habitat types for these species. We used logistic regression, with the fate of individual nests (failure or success) as the dependent variable, to evaluate the effects of various continuous landscape and vegetation variables on nesting success (SPSS, Norušis 1993). Our analyses were applied primarily to habitat types (open, mixed, and shrub/savanna) because they were distinctly different from the surrounding landscape characteristics. For a given habitat type, we limited our analyses to those species for which we had adequate numbers of nest-days (see grassland species listed in Table 1). The effects of various factors on nest survival were analyzed individually, except as noted. Results are presented as means and standard

TABLE 1. Daily nest survival (DNS) for bird species inhabiting grassland and shrub/savanna on reclaimed coal mines in Indiana during 1999 and 2000.

	n (no. successful)	ND[a]	DNS	SE
Grassland species				
Grasshopper Sparrow	41 (26)	383	0.961	0.010
Henslow's Sparrow	21 (9)	236	0.949	0.014
Field Sparrow	90 (36)	629	0.919	0.011
Dickcissel	47 (11)	369	0.903	0.016
Eastern Meadowlark	129 (58)	1450	0.951	0.006
Red-winged Blackbird	264 (74)	2439	0.923	0.005
Shrub/Savanna species				
Mourning Dove	62 (33)	816	0.962	0.007
Willow Flycatcher	30 (22)	440	0.982	0.006
American Robin	33 (12)	313	0.933	0.014
Brown Thrasher	31 (14)	251	0.932	0.016
Yellow Warbler	21 (13)	272	0.971	0.010

[a] Number of nest-days observed.

errors; the level of significance was set at 0.05.

RESULTS

During our 2-year study, we found 911 active nests of 31 species. Of these nests, 465 and 446 were found at the Chinook and Universal mines, respectively. Red-winged Blackbirds, Eastern Meadowlarks, Field Sparrows, Dickcissels, Grasshopper Sparrows, and Henslow's Sparrows were (in that order) the best represented grassland birds (Table 1). Nests of other grassland species, such as those of Ring-necked Pheasants (*Phasianus colchicus*), Sedge Wrens (*Cistothorus platensis*), and Bobolinks (*Dolichonyx oryzivorus*), were too few in number for analyses, as these species are relatively rare on the reclaimed surface mines (DeVault et al. 2002). Among the shrub/savanna species, nests of Mourning Doves (*Zenaida macroura*), Willow Flycatchers (*Empidonax traillii*), American Robins (*Turdus migratorius*), and Brown Thrashers (*Toxostoma rufum*) were found most frequently (Table 1). The nests of other savanna species were located in numbers too small for analyses, including those of Eastern Kingbird (*Tyrannus tyrannus*), Bell's Vireo (*Vireo bellii*), Song Sparrow (*Melospiza melodia*), Blue Grosbeak (*Passerina caerulea*), Indigo Bunting (*Passerina cyanea*), Orchard Oriole (*Icterus spurius*), and American Goldfinch (*Carduelis tristis*).

Daily probability of nest survival: overall estimates.—The overall estimates of DNS (all data pooled) showed considerable interspecific variation. Among grassland species (Table 1), we estimated relatively high rates of DNS (near 0.950) for Grasshopper Sparrows, Henslow's Sparrows, and Eastern Meadowlarks. Conversely, we estimated DNS of <0.925 for Dickcissels (the lowest: 0.903), Field Sparrows, and Red-winged Blackbirds. Among savanna species, Willow Flycatchers and Yellow Warblers (*Dendroica petechia*) experienced the greatest DNS (0.982 and 0.971, respectively); we also estimated a high DNS for Mourning Doves (0.962), and our DNS estimate for Brown Thrasher was the lowest (0.932).

Predation accounted for the vast majority of nest failures. In most cases, we could only guess at the identity of the predators involved because many predators do not leave conclusive evidence of their identities at depredated nests (Thompson et al. 1999, Maier and DeGraaf 2000, Pietz and Granfors 2000, Burhans et al. 2002). However, many snakes were encountered during nest searches, mainly racers (*Coluber constrictor*) and black rat snakes (*Elaphe obsoleta obsoleta*); we also encountered smaller numbers of garter snakes (*Thamnophis* spp.) and prairie kingsnakes (*Lampropeltis calligaster*). Snakes were observed consuming eggs or chicks on two occasions. Only Red-winged Blackbirds appeared to suffer any

TABLE 2. Daily nest survival (DNS) for grassland birds, by site type (open grassland, mixed, and shrub/savanna), on reclaimed coal mines in Indiana during 1999 and 2000; χ^2 statistics were determined using program CONTRAST.

Species	Habitat type	*n*	DNS	SE
Red-winged Blackbird	Open grassland	97	0.914	0.010
	Mixed	154	0.923	0.007
	Shrub/savanna	21	0.949	0.014
		χ^2 = 4.13, df = 2, P = 0.13		
Eastern Meadowlark	Open grassland	62	0.939	0.010
	Mixed	46	0.962	0.008
	Shrub/savanna	23	0.974	0.010
		χ^2 = 6.39, df = 2, P = 0.04		
Dickcissel	Open grassland	23	0.903	0.022
	Mixed	15	0.916	0.024
	Shrub/savanna	9	0.871	0.043
		χ^2 = 0.86, df = 2, P = 0.65		
Field Sparrow	Open grassland	33	0.933	0.017
	Mixed	25	0.938	0.016
	Shrub/savanna	34	0.879	0.024
		χ^2 = 4.50, df = 2, P = 0.11		
Ammodramus spp.	Open grassland	25	0.977	0.009
	Mixed	20	0.943	0.017
	Shrub/savanna	17	0.928	0.023
		χ^2 = 6.04, df = 2, P = 0.05		

weather-induced mortality (nests blown over during severe thunderstorms), and then only early in the 1999 breeding season. There were no indications of significant nutritional stress among any nestlings.

Effects of time and site.—DNS estimates (all sites pooled) did not differ between years (χ^2: all P values > 0.10) for any grassland or savanna species except Brown Thrasher ($\chi^2 = 5.70$, df = 1, $P = 0.017$). Brown Thrasher DNS was very low in 1999 (0.895 ± 0.027), but was much greater in 2000 (0.969 ± 0.015). For American Robin, there was a similar across-year trend ($\chi^2 = 3.22$, df = 1, $P = 0.072$) in DNS, which increased from 0.885 ± 0.034 to 0.951 ± 0.014.

We found a significant time-of-season effect only for Eastern Meadowlarks; in both years, our estimate of their DNS was substantially greater during the first half of the breeding season than in the second half. In 1999, their DNS decreased from 0.974 ± 0.008 to 0.919 ± 0.016 ($\chi^2 = 9.45$, df = 1, $P = 0.005$) and, in 2000, from 0.966 ± 0.009 to 0.934 ± 0.014 ($\chi^2 = 3.70$, df = 1, $P = 0.051$). When the data were pooled across years, DNS in the first and second half of the breeding season differed substantially (0.970 ± 0.006 versus 0.926 ± 0.011, respectively; $\chi^2 = 12.33$, df = 1, $P < 0.001$).

Significant differences in DNS also were observed across habitat types (Table 2). DNS for Eastern Meadowlarks was greatest in shrub/savanna habitat (0.974) and lowest in the open habitats (0.939; $\chi^2 = 6.39$, df = 2, $P = 0.041$). DNS of *Ammodramus* sparrows was higher in the increasingly open habitats ($\chi^2 = 6.04$, df = 1, $P = 0.050$). For Field Sparrows, our DNS estimates tended to be lower in the shrub/savanna habitats ($\chi^2 = 4.508$, df = 1, $P = 0.11$). DNS for Dickcissels also was lowest in the shrub/savanna habitat (0.871), but not significantly so. Logistic regression analyses of these data produced very similar results, indicating no significant interactions between habitat type and time of season, for any of the species listed in Table 2 (Wald χ^2 tests: all $P > 0.50$). DNS did not differ between mines (χ^2: all $P > 0.10$; pooling data across all study sites within a given mine) for any species listed in Table 1.

Effects of vegetation and landscape variables.—Our analyses indicated few significant associations between DNS and vegetation or landscape features. However, DNS for Eastern Meadowlarks increased with distance to forest in the shrub/savanna sites (logistic regression: b = 0.019, Wald χ^2 = 3.95, df = 1, P = 0.047). Increasing nest height also was associated with lower DNS for Field Sparrows, but only in open grassland habitats (b = −0.487, Wald χ^2 = 4.22, df = 1, P = 0.040); DNS was lower for nests in low shrubs than for those on the ground. For Red-winged Blackbirds, height of vegetation in which the nest was placed was positively associated with nesting success, but only in the mixed habitat type (b = 0.051, Wald χ^2 = 6.42, df = 1, P = 0.011). Finally, for Grasshopper Sparrows, height of the dominant vegetation within 1 m of the nest was positively associated with nesting success, but only when the data were pooled across all habitat types (b = 0.465, Wald χ^2 = 4.14, df = 1, P = 0.046). It is notable that tall fescue (either as the vegetation in which the nest was placed or as the dominant vegetation within 1 m of the nest) was not significantly associated with the DNS of any focal species.

Brood parasitism.—Relatively low rates of brood parasitism by Brown-headed Cowbirds were observed during our 2-year study. Overall, only 2.1% of grassland bird nests were parasitized by cowbirds (Table 3). Field Sparrows were the most heavily parasitized (6.4%), whereas we observed no parasitism on Henslow's Sparrows or Eastern Meadowlarks. Furthermore, of the 263 Red-winged Blackbird nests that we found, only four were parasitized. Shrub/savanna species as a group (including all species monitored) suffered a greater frequency of brood parasitism (12.0%; Table 3). Of the savanna species, Orchard Orioles and Blue Grosbeaks were most heavily parasitized.

TABLE 3. Brown-headed Cowbird parasitism of host species was infrequent on reclaimed coal mines in Indiana during 1999 and 2000.

Species[a]	n	No. Parasitized	%
Grassland			
Sedge Wren	1	0	0.0
Red-winged Blackbird	263	4	1.5
Bobolink	1	0	0.0
Eastern Meadowlark	131	0	0.0
Dickcissel	47	2	4.1
Field Sparrow	93	6	6.4
Grasshopper Sparrow	41	1	2.4
Henslow's Sparrow	21	0	0.0
Total	607	13	2.1
Shrub/Savanna			
Eastern Kingbird	9	1	11.1
Willow Flycatcher	30	0	0.0
Bell's Vireo	6	1	16.7
Yellow Warbler	21	3	14.3
Orchard Oriole	10	4	40.0
Blue Grosbeak	6	2	33.3
Indigo Bunting	4	0	0.0
American Goldfinch	6	0	0.0
Song Sparrow	8	1	12.5
Total	100	12	12.0

[a] Known egg rejectors (e.g., American Robins, Brown Thrashers) and unsuitable cowbird hosts (e.g., Mourning Doves) were not included.

DISCUSSION

Daily nest survival.—Overall estimates of DNS varied considerably across species. In general, shrub/savanna birds experienced greater rates of DNS than grassland birds (Table 1). Among grassland birds, Eastern Meadowlarks, Grasshopper Sparrows, and Henslow's Sparrows experienced relatively high rates of DNS, whereas Dickcissels, Field Sparrows, and Red-winged Blackbirds experienced lower rates of DNS. Among shrub/savanna species, Mourning Doves, Willow Flycatchers, and Yellow Warblers experienced relatively high rates of DNS, whereas American Robins and Brown Thrashers experienced relatively low rates of DNS. There were no significant differences in DNS across the two mines studied, despite the fact that these mines encompass the range of land-use patterns found within mines (Bajema and Lima 2001). There also were few significant differences in DNS across the two breeding seasons, despite the fact that the first season (1999) was relatively hot and dry, and the second season (2000) was cool and wet (only Brown Thrashers and American Robins had markedly greater DNS in 2000 than 1999). Thus, the general patterns apparent in Table 1 may be representative of the long-term situations faced by birds on the reclaimed mines of southwestern Indiana.

Ultimately, the variation that we observed in DNS was due to variation in nest predation, the primary cause of nest failure. Among grassland birds, it appears that open-cup, above-ground nesters, such as Field Sparrows, Dickcissels, and Red-winged Blackbirds, suffered greater predation rates than ground-nesting species (Eastern Meadowlarks and *Ammodramus* sparrows; Table 1). During both field seasons, we estimated greater DNS for Eastern Meadowlarks during the first half of the breeding season than during the second half. This time-of-season effect may reflect the fact that Eastern Meadowlarks began nesting in April before snakes became fully active. No other temporal patterns in DNS were apparent among other grassland species.

Open-cup nesting was not uniformly associated with greater rates of nest predation, because all shrub/savanna species in this study are open-cup nesters, and many experienced high rates of DNS (Table 1). The relatively low rate of nesting success among American Robins and Brown Thrashers was due to extremely high levels of nest predation during 1999 (which was not observed in 2000). Why only these two species experienced different levels of predation across years is not clear; however, because robins and thrashers nested in very similar sites in the shrub/savanna habitat (interior portions of larger trees), they likely experienced the same change in the predatory environment across years.

Significant associations between DNS and various vegetation and landscape-level features were few, and provided relatively little insight into the predation processes that influenced DNS. We note, however, that for many species we located too few nests for our analyses to detect subtle effects. Regardless, the significant increase in DNS with increasing distance from the forest—exhibited only in Eastern Meadowlarks in the shrub/savanna habitat—was consistent with the results of other studies (e.g., Johnson and Temple 1990) that implicated forest-edge predators as major agents of nest failure (recall that our shrub/savanna sites were adjacent to forested habitat). The lack of an effect of distance-to-forest in the open grassland and mixed study sites may reflect the relative isolation of these sites from forested habitat (*cf.* Paton 1994). The relatively high rates of DNS for *Ammodramus* sparrows in the open grassland habitats (Table 2) also may reflect the isolation from forested habitat. Nevertheless, there was no association between distance-to-forest and DNS for any other species in the shrub-savanna sites. Furthermore, the overall nesting success of Eastern Meadowlarks was actually greater in the shrub/savanna habitat than elsewhere (Table 2).

Across studies, a consistent picture of the effects of vegetation and landscape variables on nesting success of many grassland species has yet to emerge. For example, Johnson and Temple (1990) observed increased nest predation for grassland passerines when their nests were located near wooded edges. Winter et al. (2000) found that, for artificial nests, fragment size and vegetation characteristics were better predictors of survival than distance to habitat edge; however, Henslow's Sparrow nests placed within 50 m of an edge were not as successful as those at greater distances from forest edge. For Dickcissels, distance to habitat edge also appeared to have little effect on daily survival in prairie habitats (Hughes et al. 1999, Winter et al. 2000). Burhans et al. (2002) observed that Field Sparrows nesting in old fields had greater success when nest height was >3 m above ground; however, Best (1978) suggested that Field Sparrows were more successful when nests were near the ground or in relatively tall vegetation. Pribil (1998) did not detect a relationship between nest success and vegetation features for Red-winged Blackbirds.

Brood parasitism.—Brood parasitism was minimal in our focal species, especially when compared with the high frequency of parasitism reported in midwestern forest fragments (e.g., Robinson et al. 1995). For grassland birds, only 2.1% of nests were parasitized. The frequency of parasitism for Red-winged Blackbirds at our reclaimed surface coal mines (1.5%) markedly contrasts with the parasitism frequency of ≥30% for this species in other habitats and areas to the west of our study sites (Yasukawa and Searcy 1995, Clotfelter and Yasukawa 1999). Kershner (2001) and Walk (2001) reported similarly low frequency of parasitism for grassland birds nesting in restored prairies in nearby eastern Illinois (see also Robinson and Herkert 1997, Kershner and Bollinger 1998). Perhaps the frequency of grassland bird parasitism is generally greater well to the west of Indiana (Johnson and Temple 1990, Zimmerman 1993, Davis 2003; but see Winter 1999, Winter et al. 2004). In any case, the low frequency of cowbird parasitism for grassland birds of western Indiana and eastern Illinois supports

TABLE 4. Daily nest survival for grassland birds on reclaimed coal mines in Indiana during 1999 and 2000 was similar to that recorded at other midwestern grassland sites.

Species	Kansas CRP fields[a]	Prairie (MO)[b]	Big Oaks NWR (IN)[c]	Iowa CRP fields (egg, nestling stage)[d]	Restored prairie (IL)[e]	Reclaimed coal mines (IN)[f]
Red-winged Blackbird	—	—	—	0.943, 0.916	0.954	0.923
Eastern Meadowlark	—	0.940	—	—	0.953	0.951
Dickcissel	0.922	0.940	—	0.951, 0.874	0.941	0.903
Field Sparrow	—	—	0.919	—	0.955	0.919
Grasshopper Sparrow	—	0.930	—	0.957, 0.937	0.913	0.961
Henslow's Sparrow	—	0.950	0.947	—	—	0.949

[a] Hughes et al. (1999), [b] Winter and Faaborg (1999), [c] Robb et al. (1998), [d] Patterson and Best (1996), [e] Kershner (2001) and Walk (2001); [f] this study.

the idea that cowbirds in the eastern United States focus on forested habitats (Hahn and Hatfield 1995). Indeed, Brown-headed Cowbird is among the rarest passerine species inhabiting reclaimed coal mines in Indiana (DeVault et al. 2002).

Shrub/savanna species underwent greater rates of parasitism than grassland species (Table 3), but it was still much lower than that typically observed in forested habitats across Indiana and Illinois (e.g., Robinson et al. 1995). Among the focal savanna species (Table 1), only Yellow Warblers were parasitized to a substantial degree (Table 3). Note, however, that three of our focal savanna species are either inappropriate cowbird hosts (Mourning Doves) or egg rejectors (American Robins and Brown Thrashers). Parasitism appeared to be greater for some non-focal savanna species (e.g., Orchard Orioles and Blue Grosbeaks; Table 3), but we found too few nests to reach a conclusion concerning their susceptibility to parasitism. We suspect that greater rates of cowbird parasitism in our shrub/savanna sites reflected their proximity to forested habitat (Hahn and Hatfield 1995).

Conservation implications.—Our data suggest that reclaimed surface coal mines are no more likely to represent reproductive traps than are other habitats studied to date. We base this view on a comparison of our results with those from comparable studies across the midwestern United States. DNS within reclaimed coal mine grasslands at our study sites is broadly comparable to that in other midwestern grasslands (Table 4). The most comparable study is one that took place in large blocks of restored prairies in nearby eastern Illinois (Kershner 2001, Walk 2001). DNS of Eastern Meadowlarks in Illinois was essentially identical to that observed in our reclaimed mine sites (Table 4). Dickcissels and Field Sparrows experienced greater nest success at the Illinois sites than at our sites, whereas Grasshopper Sparrows experienced greater success at our mine sites (few Henslow's Sparrow nests were found at the Illinois site). Similar to what we found in our study, Red-winged Blackbirds in Conservation Reserve Program (CPR) fields of Iowa experienced poor to mediocre nesting success, Dickcissels experienced low success (with very low survival in the nestling stage), and Grasshopper Sparrows had relatively high rates of success (Patterson and Best 1996). Dickcissels also may not be doing well in Kansas or Missouri CRP fields (Hughes et al. 1999, Winter and Faaborg 1999). Nesting success of Field and Henslow's sparrows at the Big Oaks National Wildlife Refuge (formerly the Jefferson Proving Ground) in southeastern Indiana is virtually identical to that of birds nesting on reclaimed surface coal mines (Robb et al. 1998). Furthermore, survival estimates for Henslow's Sparrows across the three relevant studies (Robb et al. 1998, Winter and Faaborg 1999; this study) were remarkably similar and relatively high, indicating that this species is probably doing reasonably well where it is still nesting. Similarly, Monroe and Ritchison (2005) reported comparable levels of nesting success for Henslow's Sparrows on reclaimed mines and unmined grasslands in western Kentucky, and suggested that reclaiming surface mines could help stabilize the population decline of Henslow's Sparrows. We suspect that similar conclusions also could be drawn for some savanna species on reclaimed mines, but comparable data are not yet available with which to make analogous comparisons.

Reclaimed mines of the Midwest provide a unique opportunity in avian conservation, especially for the management of grassland birds. Many of the reclaimed mines are >2,000 ha, larger than most (if not all) remaining prairie fragments in Indiana and Illinois, and contain large populations of several bird species of concern (Bajema et al. 2001, DeVault et al. 2002, Ingold 2002). The nesting success of key species (e.g., Henslow's Sparrows and Grasshopper Sparrows) at these reclaimed mines is comparable with that in nonmined grassland habitats. A feature that should make reclaimed midwestern surface coal mines attractive from a management perspective is that they are usually owned by a single entity. Furthermore, most reclaimed mines are typically not very productive as agricultural areas. These factors combined make possible the acquisition or management of large grassland-dominated habitats. Few such opportunities currently exist in the eastern United States.

ACKNOWLEDGMENTS

The U.S. Fish and Wildlife Service, the U.S. Geological Survey, and the Ohio River Valley Ecosystem Group provided financial support for this project. We are grateful to the following individuals for allowing us full access to reclaimed mine properties: A. Eicher and S. McGarvie of Peabody Coal, R. Ronk of the Indiana Department of Natural Resources, M. Krieger at Universal Mine, and L. Nelson of the Midwest Coal Company. We also thank G. S. Bakken, M. T. Jackson, and P. E. Scott for valuable help and advice. Special thanks go to R. Gushee, J. Mozingo, C. Roever, B. Thomas, and A. Worthington for their competent fieldwork and keen nest-finding abilities. We are grateful to M. D. Carey and two anonymous reviewers for helpful comments that improved this manuscript.

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The Wilson Journal of Ornithology 118(4):547–551, 2006

DIFFERENTIAL TIMING OF WILSON'S WARBLER MIGRATION IN ALASKA

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ABSTRACT.—We examined age- and sex-related differences in the timing of Wilson's Warbler (*Wilsonia pusilla pileolata*) migration at four locations in Alaska: Fairbanks, Tok, Mother Goose Lake, and Yakutat. We captured Wilson's Warblers with mist nets for ≥5 years during spring (northbound) and autumn (southbound) migration. In spring, males passed through our two northernmost sites—Tok and Fairbanks—earlier than females. During autumn, timing of adult migration did not differ by sex, but immatures passed through earlier than adults at all four sites. During previous studies of autumn passage sampled at lower latitudes, the lack of age-related differences in migration timing could be attributed to adults migrating faster than immatures (i.e., if immatures from higher latitudes began migration earlier than the adults, then the adults may have caught up to them at lower latitudes) or to the mixing of breeding populations from different locales. Autumn migration of adults and immatures netted at our two southernmost sites, both coastal locations, preceded migration at our two interior sites. These site-specific differences in the timing of autumn migration are likely the result of our coastal stations sampling birds that breed farther south and arrive earlier than birds breeding in more northerly regions of Alaska (and sampled at our interior stations). Early-arriving populations are likely able to complete their breeding season activities earlier and, subsequently, initiate their autumn migration earlier. *Received 29 July 2005, accepted 5 May 2006.*

Age- or sex-related differences in timing of migrant passage have been documented at several locations in North America (see reviews by Gauthreaux 1982, Woodrey 2000). Analyses of between-sex variation in the timing of spring migration have shown that males of several North American passerine species migrate prior to females (Francis and Cooke 1986, Yunick 1988, Otahal 1995, Yong et al. 1998, Swanson et al. 1999). Studies documenting age-class differences in the timing of autumn migration have revealed varied patterns. Immature Wilson's Warblers (*Wilsonia pusilla*) preceded adults by 9 days in southwestern Idaho (Carlisle et al. 2005a); 10 days at Yakutat, Alaska (Andres et al. 2005); and 13 days at Fairbanks, Alaska (Benson and Winker 2001). The autumn migration timing of adult and immature Wilson's Warblers did not differ in South Dakota (Dean et al. 2004) or in the riparian forest of the middle Rio Grande in New Mexico (Yong et al. 1998).

We selected the Wilson's Warbler to examine differential migration timing because it is a relatively abundant migrant and is sexually dichromatic. Wilson's Warblers breed throughout Alaska and winter in the southern United States, Mexico, and Central America (Ammon and Gilbert 1999). *W. p. pileolata* is the only subspecies known to range into Alaska (American Ornithologists' Union 1957, Gibson and Kessel 1997).

The geographic location of Alaska, relative to the continental landmass, provides an opportunity to study the passage of migrants near where they terminate their spring migration and initiate their autumn migration. Our objectives were to use data from four widely dispersed migration banding stations in Alaska to examine differences in the timing of Wilson's Warbler migration. Our specific objectives were to determine (1) between-sex differences in the timing of spring migration, (2) between-age differences in the timing of autumn migration, and (3) among-site differences in the timing of autumn migration.

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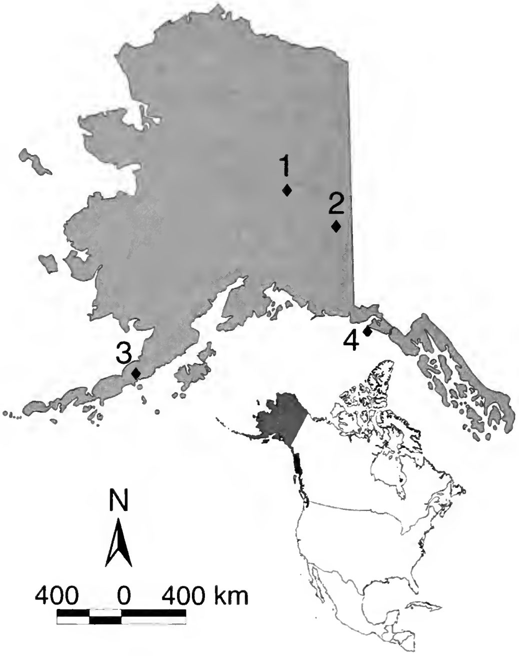

FIG. 1. Location of four migration monitoring stations in Alaska: (1) Fairbanks, (2) Tok, (3) Mother Goose Lake, and (4) Yakutat, 1992–2000.

METHODS

Study sites.—We analyzed data from four migration stations operated for ≥5 years during 1992–2000. Fairbanks and Tok were operated in spring and autumn, and Yakutat and Mother Goose Lake were operated only in the autumn. The Fairbanks banding station, operated by the Alaska Bird Observatory on the Creamer's Field Migratory Waterfowl Refuge (64° 50′ N, 147° 50′ W), and the Tok banding station (63° 22′ N, 143° 12′ W), operated by the Tetlin National Wildlife Refuge, are located in interior Alaska in the Tanana River Valley (Fig. 1). The Yakutat station, operated by the U.S. Fish and Wildlife Service, is on the Gulf of Alaska coastline ~300 km northwest of Juneau (59° 30′ N, 139° 40′ W; Fig. 1). The Mother Goose Lake station (57° 11′ N, 157° 15′ W), operated by the Alaska Peninsula/Becharof National Wildlife Refuge Complex, lies west of the Aleutian Mountain Range in southwestern Alaska, ~165 km southwest of King Salmon (Fig. 1).

We used 2.6- × 12-m nets with 30-mm mesh at all stations; specific operation details are provided in Table 1. The netting period at all stations spanned the entire duration of Wilson's Warbler migration. Our studies were designed to capture a wide suite of passerine species, many of which pass through study sites earlier and depart later than Wilson's Warblers.

Ageing and sexing.—At all locations during fall migration, age was determined by degree of skull ossification (Pyle 1997). During spring at Fairbanks and Tok, and during fall at Yakutat and Mother Goose Lake, birds were sexed by plumage and morphometric characteristics (Pyle 1997). During autumn at Fairbanks and Tok, birds were sexed using the following discriminant function, developed from known-age Alaskan birds (Weicker and Winker 2002), whereby 96% of known-age birds were classified correctly:

$$\begin{aligned} D = {} & 0.9189 \text{ cap category} \\ & + 0.1800 \text{ cap length} \\ & + 0.0977 \text{ tail length} \\ & + 0.0938 \text{ wing chord} \\ & - 13.9426, \end{aligned}$$

where D is the discriminant function, cap category separates caps into one of four classes (ranging from solid olive-green to solid

TABLE 1. Spring and autumn mist-netting efforts to capture migrant Wilson's Warblers at four banding stations in Alaska, 1992–2000.

Station	Season	Years	Period	No. nets	Time	Total net hr
Fairbanks	Spring	1992–2000	25 Apr–15 Jun	22–50	06:00–13:00	81,736
	Autumn	1992–2000	15 Jul–30 Sep	22–50	sunrise + 7 hr	114,053
Tok	Spring	1994–1998	late Apr–early Jun	20–24	sunrise + 6 hr	22,707
	Autumn	1993–2000	early Aug–late Sep	20–24	sunrise + 6 hr	49,322
Mother Goose Lake	Autumn	1994–2000	1 Aug–22 Sep	10–15	sunrise + 6 hr[a]	11,018
Yakutat	Autumn	1994–1999	1 Aug–5 Oct	10–15	sunrise + 6 hr	23,256

[a] Nets were opened 0.5 hr after sunrise.

TABLE 2. Median passage dates of Wilson's Warbler at four locations in Alaska: Fairbanks (1992–2000), Tok (1993–2000), Yakutat (1994–1999), and Mother Goose Lake (1994–2000).

		Adult between-sex differences					Between-age-class differences				
		Males		Females			Immatures		Adults		
Season	Site	Date[a]	*n*	Date[a]	*n*	*z*	Date[a]	*n*	Date[a]	*n*	*z*
Spring											
	Fairbanks	143	105	148	143	4.40**[b]					
	Tok	142	771	150	450	18.33**					
Autumn											
	Fairbanks	243	58	253	28	1.56	230	1,009	243	105	9.52**
	Tok	242	195	240	36	1.29	230	1,185	241	616	17.71**
	Yakutat	228	73	228	38	0.70	222	374	228	111	5.60**
	Mother Goose Lake	234	160	234	50	0.32	225	10,481	235	287	17.29**

[a] Median Julian date of passage.
[b] Double asterisk indicates $P < 0.001$.

black), and cap length is the extent of black feathers from the front to the back of the head. For our analyses, we included only records with ≥75% probability that individuals were sexed correctly.

Definition of migrants.—In analyses for all sites, we included only first captures of birds. Based on two criteria, we eliminated individuals that may not have been migrating at the time of capture: (1) birds recaptured >7 days after first capture and (2) locally fledged birds (i.e., birds retaining >60% of their juvenal plumage). We did not specifically remove females with brood patches because this could potentially bias the retention of males and elimination of females, and affect our between-sex comparisons. No females with brood patches were captured at Fairbanks, Tok, or Yakutat, and only nine such individuals were captured and included in the data set from Mother Goose Lake. It is possible that birds not migrating at the time of capture were included in our analyses, resulting in an early-biased median date of autumn passage. However, considering the relatively few birds netted in summer compared to the vast numbers captured during the brief and intense migration pulse, we suspect the numbers of breeding birds included in these analyses were small. If some non-migratory birds were included in these analyses, they likely affected the data from each station and, therefore, should not have affected our among-site comparisons.

Data analysis.—We tested for age-, sex-, and site-related differences in median passage dates by using Mann-Whitney *U*-tests. For two reasons, we did not standardize by unit of netting effort. First, standardizing by unit of effort can artificially inflate or deflate sample sizes, which, in turn, can affect the power of a test (see examples in Benson and Winker 2001). Second, standardizing by unit of effort was not necessary in these analyses because even in Fairbanks, where there were some netting-effort inconsistencies in earlier years, net hr over a given season had a uniform distribution when all years were combined (see Benson and Winker 2001).

RESULTS

During spring migration, males preceded females by 5 days at Fairbanks ($Z = 4.40$, $n = 248$, $P < 0.001$; Table 2) and by 8 days at Tok ($Z = 18.33$, $n = 1{,}221$, $P < 0.001$; Table 2). In autumn, we found no between-sex difference in the timing of adult migration at any location (Table 2). However, immatures consistently preceded adults at all locations: by 13 days at Fairbanks ($Z = 9.52$, $n = 1{,}114$, $P < 0.001$), 11 days at Tok ($Z = 17.71$, $n = 1{,}801$, $P < 0.001$), 6 days at Yakutat ($Z = 5.60$, $n = 485$, $P < 0.001$), and 10 days at Mother Goose Lake ($Z = 17.29$, $n = 10{,}768$, $P < 0.001$; Table 2). Passage of both adults and immatures was significantly earlier at the two coastal sites than at the two interior sites (all $Z \geq 7.84$, $P < 0.001$). Wilson's Warblers also passed through Yakutat significantly earlier than they did at Mother Goose Lake (all

$Z \geq 5.23$, $P \leq 0.001$). There was no significant difference between the passage dates at Fairbanks and Tok.

DISCUSSION

Basic patterns in the timing of migration were similar at all four migration stations in Alaska. In spring, the earlier passage of male Wilson's Warblers, compared with females, was similar to results found by Francis and Cooke (1986) and Yong et al. (1998). These results were expected because of the selective pressures that favor males to arrive early and obtain a high-quality territory, whereas females likely benefit by arriving later when resources are more predictable (see review by Francis and Cooke 1986).

Immature Wilson's Warblers migrate southward from Alaska significantly earlier than adults, most likely because they do not undergo the full prebasic molt that adults must complete before migration (Dwight 1900). Adults, however, compensate for their later migration by migrating with greater mass and fat stores (Andres et al. 2005, Benson and Winker 2005). The differences in age-related migration timing among Wilson Warblers in fall may not be detectable at lower latitudes (e.g., Yong et al. 1998, Dean et al. 2004) because immatures may migrate at slower rates due to their inability to forage as efficiently as adults. During fall migration in New Mexico, immature Wilson's Warblers had lower fat scores than adults, but age-class differences in mass and rates of mass gain have not been detected at other locations for this species (Jones et al. 2002, Carlisle et al. 2005b).

The among-site differences in median dates of autumn passage were not surprising. The onset of winter can vary substantially throughout the large and mountainous state of Alaska, and populations originating from regions with briefer summers are likely to depart earlier. Stopover ecology of Wilson's Warblers is also influenced by habitat (Hutto 1985, Skagen et al. 1998), but we did not measure the effect of this variable at the locations studied.

We currently lack sufficient information for defining the breeding ranges of populations sampled at our four study sites; however, we hypothesized that samples from interior sites represented different populations than those sampled at coastal sites because large mountain ranges separate the southern coast of Alaska from the state's interior. Isotopic ratios of Wilson's Warblers breeding in western North America indicate that coastal breeders overwinter in western Mexico and those that breed farther inland and at higher elevations overwinter in eastern Mexico (Clegg et al. 2003). However, a few recoveries of birds banded at Mother Goose Lake indicate that birds occurring at that site may represent populations that winter in both eastern and western locations.

ACKNOWLEDGMENTS

Funding for this project was provided by the Alaska Bird Observatory, Alaska Department of Fish and Game, Alaska Peninsula/Becharof National Wildlife Refuge, Earthwatch Institute, Tetlin National Wildlife Refuge, and U.S. Fish and Wildlife Service (Region 7) Migratory Bird Management, and Alaska Department of Natural Resources. These studies would not have been possible without the many staff and volunteers that contributed countless hours capturing and banding birds. We especially thank B. Browne, T. J. Doyle, A. R. Ajmi, C. Adler, T. Burke, K. Convery, C. R. Davis, D. Dewhurst, N. DeWitt, R. C. Egan, T. Eskelin, J. Foster, N. Gregory, R. I. Frey, J. Klima, A. L. Lancaster, K. W. Larson, M. Margulies, R. C. Means, J. Melton, R. Moore, H. Moore, R. K. Papish, T. H. Pogson, G. Ruhl, M. Sardy, D. Shaw, K. M. Sowl, S. K. Springer, H. K. Timm, L. Wells, and D. L. Williams. We also thank G. Collins for preparing the map and P. J. Heglund for reviewing an earlier version of the manuscript. Many thanks to D. L. Swanson and an anonymous reviewer for comments that improved the manuscript.

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The Wilson Journal of Ornithology 118(4):552–557, 2006

NESTING SUCCESS OF WESTERN BLUEBIRDS (*SIALIA MEXICANA*) USING NEST BOXES IN VINEYARD AND OAK-SAVANNAH HABITATS OF CALIFORNIA

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ABSTRACT.—Loss of oak woodlands to vineyard development in California is a growing concern to conservationists. Analyzing breeding performance of birds that nest in and around vineyards versus those that nest in nearby native habitat can provide information on the suitability of vineyard environments to birds. We placed predator-protected nest boxes in vineyard and oak-savannah habitats and monitored nest-box occupancy, nesting success, and life history characteristics of Western Bluebirds (*Sialia mexicana*) that used the boxes. Western Bluebirds were common occupants in both habitats, occupying >50% of available nest boxes. Analysis using program MARK revealed that nest survival was not associated with habitat type; however, clutch size was greater and nests were initiated earlier in vineyard than in oak-savannah habitat. Our results suggest that when naturally occurring nest sites are limiting, vineyards could be converted to good breeding habitat for Western Bluebirds with the addition of nest boxes. Nest boxes, however, should not be viewed as a remedy for the chronic problem of habitat loss and degradation. *Received 27 June 2005, accepted 5 May 2006.*

The loss of oak woodland habitat to vineyard expansion is a growing concern in California (Zack 2002). More than 100 bird species breed in California's oak woodlands (Verner 1980), making the loss and degradation of this habitat particularly problematic. In San Luis Obispo County, California, land used for viticulture increased from 4,008 to 10,851 ha between 1996 and 2000 (Mummert et al. 2002). Conservationists generally view vineyards as sub-optimal habitat for birds due to the potential impacts of pesticides and herbicides, habitat fragmentation, attraction of nonnative bird species and predators, loss of wildlife shelter and forage, and changes to the native plant community. The ecological consequences of this large-scale habitat conversion, however, are not well understood.

The addition of nest boxes has been found to augment nesting success and breeding densities of secondary cavity-nesting bird (SCNB) species in altered habitats (Brawn and Balda 1988, Twedt and Henne-Kerr 2001, LeClerc et al. 2005). In golf course habitats, Le Clerc et al. (2005) found that nest boxes provide high-quality nesting habitat for Eastern Bluebirds (*Sialia sialis*). Little is known, however, about the nesting success of SCNB species that breed in vineyards compared to those that breed in native oak woodland, and it is unknown whether vineyards that feature nest boxes provide adequate breeding habitat for the closely related Western Bluebird (*Sialia mexicana*). The main objective of our study was to compare breeding performance and life history characteristics of Western Bluebirds using nest boxes in a minimum-impact vineyard with bluebirds using nest boxes in native oak-woodland habitat.

METHODS

Study site and study species.—We studied Western Bluebirds on the Santa Margarita Ranch, approximately 25 km north of San Luis Obispo in central coastal California, during the breeding seasons of 2003 and 2004. This privately owned, 5,700-ha property surrounding the town of Santa Margarita (35° 23.39′ N, 120° 36.55′ W) features a working cattle operation and 1,000 acres comprising the Cuesta Ridge Vineyard. The dominant tree species on the study area are valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), coast live oak (*Q. agrifolia*), California foothill pine (*Pinus sabiniana*), and willow (*Salix* spp.). The understory is predominantly open and consists primarily of annual grasses and forbs, including ryegrass (*Lolium* spp.), wild

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oat (*Avena* spp.), brome (*Bromus* spp.), milkweed (*Asclepias* spp.), and exotic weeds such as star-thistle (*Centaurea* spp.) and other thistles (*Cirsium* spp.). Unlike typical California vineyards, which comprise large, contiguous tracts of trellised vines, the Cuesta Ridge Vineyard is a minimum-impact vineyard characterized by smaller planted areas that follow contours of the surrounding hills and the retention of relict oak trees (*Quercus* spp.) in, and adjacent to, the vineyard.

The Western Bluebird is the most common SCNB species on the study area. It is migratory, returning in late winter and initiating nest building in early March. This insectivorous species is monogamous and is known to rear one to two broods over the spring and summer, with both parents caring for the young (Guinan et al. 2000). Other SCNB species on the study area included Tree Swallow (*Tachycineta bicolor*), Violet-green Swallow (*Tachycineta thalassina*), Ash-throated Flycatcher (*Myiarchus cinerascens*), and House Wren (*Troglodytes aedon*).

Nest boxes.—During January and February 2003, we placed 120 nest boxes in each of two habitat types on the Santa Margarita ranch: oak-savannah and vineyard. The oak-savannah habitat was open oak woodland (≤10% canopy coverage) characterized by grassland and scattered oak trees. We placed vineyard nest boxes ≤12 m outside of the vineyard edge because placing nest boxes in the middle of a vineyard matrix would have interfered with daily vineyard management. To reduce anthropogenic disturbance and minimize home-range overlap between bluebird pairs nesting in vineyard versus oak-savannah habitats, we placed oak-savannah nest boxes ≥300 m from any vineyard edge.

Boxes were constructed of rough-cut cedar fence board using a plan developed by the North American Bluebird Society and featured in Berger (2000). The boxes were modified such that they opened from the top instead of from the side. In each habitat type, we randomly selected 30 points that were then used as starting points for lines of four nest boxes. Each line featured two nest boxes with large-diameter entrance holes (3.9 cm) and two boxes with small-diameter entrance holes (3.2 cm). Entrance hole sizes were chosen to promote nesting by native SCNBs and to prevent nesting by nonnative cavity nesters, such as European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*). Using metal hose clamps, we mounted two boxes of different entrance hole sizes back-to-back on a single 2.4-m-high T-post; the other two boxes were mounted singly on two separate T-posts. To minimize the chances of nest predation, we used bailing wire to fasten a 61-cm-long, 5.1-cm-diameter PVC pipe to each T-post directly under the nest box. Foam sealant was injected into the core of the PVC pipe to prevent snakes and small mammals from climbing between the post and the PVC. The mounted boxes were then placed in lines of three T-posts spaced 100 m apart to decrease nest-site competition between Western Bluebird pairs (Perren 1994). The four boxes were placed such that two entrance holes faced east and two faced west. Box placement (paired or single) and direction (east or west) were assigned randomly.

Nest box monitoring.—In 2003, we monitored nest boxes every 7–14 days throughout the nesting season, which was sufficient for accurately determining rates of nest-box occupancy but not nest stages and fates. From March to May 2004, we inspected each nest box at least every 7–10 days. Once we found a nest box with signs of nesting activity, we determined the initiation date and monitored the nest box at 3–4 day intervals to determine its status; when stage transitions (e.g., onset of incubation, hatching, and fledging) were expected, we monitored nests every 1–2 days (Ralph et al. 1993, Martin et al. 1997). To reduce the possibility of forced fledging (Keyser et al. 2004), we did not open nest boxes after Western Bluebird nestlings were 14 days old. For nest boxes with bluebird nestlings older than 14 days, we evaluated the nest status by observing parental behavior and listening for nestlings in the box. We monitored each Western Bluebird nest until all young had fledged or the nest had failed. We considered a nest successful if it was empty within 2 days of the calculated fledging date and there was no sign of predation and/or if we observed fledglings in the area (Martin et al. 1997). We checked each nest 1–2 days after the calculated fledging date to confirm the presence of a family group in the area.

Habitat measurements.—In 2004, we measured nine habitat variables at each nest box after the young fledged or the nest failed. Many of the measurements were based on those used in the BBIRD protocol (Martin et al. 1997). Variables included slope, aspect, and orientation of the nest-box entrance, distance to the nearest vines, and the distance to and the height and DBH of the nearest tree. Within 10 m of the nest box, we used a spherical densiometer to measure percent canopy cover and we visually estimated the percent cover of shrubby, downed woody material, forbs, and grasses. We defined "distance to nearest perch" as the distance to the nearest tree in oak-savannah habitat and distance to nearest vines in vineyard habitat. This variable provided an index of perch-site availability in the two habitats.

We measured the interior temperature of four nest boxes in 2004 (two in vineyard and two in oak-savannah habitat) by fastening a HOBO H8 (Onset Computer Corp., Bourne, Massachusetts) temperature data logger to the T-post and extending a thermocouple inside the nest box. For each box, temperature readings were recorded every 15 min during the entire nestling stage (37–39 days).

Statistical analyses.—We used a χ^2 goodness-of-fit test (Zar 1996) to compare observed versus expected nest-box occupancy in oak-savannah and vineyard habitat. We used the nest survival model in program MARK (White and Burnham 1999) to model effects of biologically relevant factors, such as habitat (vineyard and oak-savannah) on daily survival rate (Dinsmore et al. 2002). Model A included nest survivorship as a function of the grouping variable (habitat), and model B assumed constant survivorship over time. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to compare the set of *a priori* candidate models (Burnham and Anderson 1998). The best model was selected by evaluating the degree of support for each model using the AIC_c values and normalized Akaike weights (w_i; Burnham and Anderson 1998). The Akaike weight evaluates the strength of evidence for each model; the higher the weight, the stronger the model (Burnham and Anderson 1998). We examined the relationship between mean clutch size and initiation date using a linear regression and tested the significance of the regression with an *F*-test (Zar 1996).

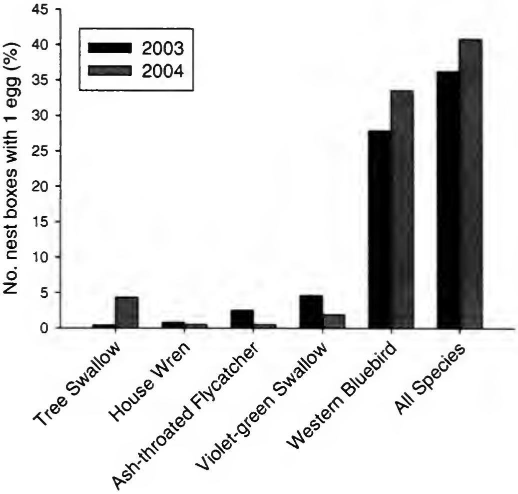

FIG. 1. Nest-box occupancy (%) of 120 nest boxes used by secondary cavity-nesting bird species on the Santa Margarita Ranch, San Luis Obispo County, California, in 2003 and 2004.

We used a Shapiro-Wilk statistic (SPSS Institute, Inc. 2003) to test all variables for normality. We then used Mann-Whitney *U*-tests (Zar 1996) to test for habitat-based differences in clutch initiation date, clutch size, number of eggs hatched, number of young fledged, slope, percent canopy cover, and distance to the nearest perch.

RESULTS

Nest box occupancy.—Western Bluebirds were the most common nest box occupants across habitats and years (Fig. 1). Western Bluebirds occupied 27.9% and 33.6% of all nest boxes in 2003 (n = 240) and 2004 (n = 208), respectively (Fig. 1). Nest boxes with the smaller diameter entrance hole were unavailable to bluebirds; therefore, considering only available boxes, bluebirds occupied 55.8% of the boxes in 2003 and 67.3% in 2004. In 2004, Western Bluebirds used nest boxes in oak-savannah and vineyard habitats in proportion to their availability (χ^2 = 0.91, df =1, P = 0.34).

Nesting success.—In 2004, we monitored 70 Western Bluebird nests (n = 39 in vineyard and n = 31 in oak-savannah). In program MARK, model A (habitat) estimated daily nest survival for the nesting period (i.e., egg-

TABLE 1. Variables (mean ± SE) describing nesting success of Western Bluebirds at the Santa Margarita Ranch, San Luis Obispo County, California, 2004.

Variable	Habitat		*P*-value
	Vineyard	Oak-savannah	
Number of nests	39	31	•
Clutch size	5.28 ± 0.08	4.97 ± 0.12	0.040
Number of nestlings per nest	4.90 ± 0.14	4.63 ± 0.21	0.465
Number of fledglings per nest	4.69 ± 0.14	4.63 ± 0.24	0.799
Initiation date (days since 1 January)	88.61 ± 1.56	92.58 ± 1.48	0.053

laying to fledging) at 0.995, and model B (constant survivorship) estimated it at 0.998. Furthermore, AICc values for model A (100.162) and model B (100.729) were similar, indicating that habitat type did not affect the survival of Western Bluebird nests on the Santa Margarita Ranch. Of the 70 nests, 10 (14%) failed, including only two (3%) probable predation events: one nest appeared to be depredated during the nestling stage by a snake, and ants swarmed the other during the incubation stage. The other eight (11%) failed nests contained either dead chicks or cold eggs, and we assumed that they were abandoned. At least one chick fledged from each of the remaining 60 (86%) nests.

Life-history characteristics.—Clutch size for many avian species has been found to decline over the course of the breeding season (Perrins and McCleery 1989, Hochachka 1990, Winkler and Allen 1996). In 2004, there was not a significant relationship between mean clutch size and initiation date for Western bluebird nests across treatments (r^2 = 0.11, df = 5, $F_{1,4}$ = 0.51, P = 0.51). Clutch sizes were larger in the vineyard than in oak-savannah (5.28 ± 0.08 versus 4.97 ± 0.12; Mann-Whitney U = 461.00, P = 0.040) and nests were initiated significantly earlier in vineyard habitat than in oak-savannah (Mann-Whitney U = 400.50, P = 0.036; Table 1). However, we found no statistically significant difference in number of nestlings (Mann-Whitney U = 473.50, P = 0.47) and number of fledglings (Mann-Whitney U = 416.00, P = 0.80) for nests in vineyard versus oak-savannah in 2004 (Table 1).

Habitat measurements.—Mean percent canopy cover around the nest boxes did not differ by habitat (5.73 ± 3.44 in oak-savannah versus 6.28 ± 3.14 in vineyard; Mann-Whitney U = 604.00, P = 0.95). We found a difference in mean distance to perch site (Mann-Whitney U = 84.5, $P < 0.001$) between nests in vineyard and oak-savannah; on average, perch sites were closer to nest boxes in the vineyard (11.44 ± 0.39) than in the oak-savannah (35.64 ± 4.21) habitat. Mean maximum temperature in nest boxes was 28.50° C ± 0.63 in oak-savannah and 28.53° C ± 0.65 in vineyard habitat. Mean minimum temperature in nest boxes was 6.22° C ± 0.27 in oak-savannah and 6.14° C ± 0.27 in vineyard habitat. Mean maximum temperature (t-test: t = 0.042, df = 74, P = 0.97) and mean minimum temperature (t = −0.232, df = 74, P = 0.82) inside the nest box over the nestling period did not differ between habitat types.

DISCUSSION

The results of this study indicate that vineyard habitat, with its limited availability of naturally occurring nest sites, could be converted to good breeding habitat for Western Bluebirds with the addition of nest boxes. In the two habitat types, Western Bluebirds were the most common nest-box occupants (>55%). In 2004, nest survival was high across habitats; at least one chick fledged from 86% of the nests. It should be noted, however, that predator guards were included on all of our nest boxes, as they are a common component of many commercially available nest-box designs, and the high nest survival and fledging rate that we observed could have been an effect of the predator guards. Thus, the high rate of nest survival that we report should be interpreted cautiously.

Clutch initiation date and clutch size differed between bluebirds nesting in vineyard versus oak-savannah habitat. Bluebirds nesting in the vineyard initiated nesting earlier and laid larger clutches than those in oak-savannah habitat. Habitat differences in food supply have been shown to affect the timing of egg laying and clutch size among passerines (Blondel et al. 1993, Siikamaki 1995), and the predictable water supply provided by daily irrigation at Cuesta Ridge Vineyard may have supported a larger insect population in the vineyard. In turn, this could have allowed female bluebirds to start laying earlier and to lay more eggs. There was no significant difference, however, between the two habitats in terms of number of nestlings or young fledged.

Nest boxes in both vineyard and oak-savannah habitats did not differ with respect to percent canopy cover or interior nest-box temperatures. However, the Cuesta Ridge vineyard was structurally different from the majority of vineyards in San Luis Obispo County: it was composed of smaller areas of vines that encompassed large valley oaks adjacent to large patches of native oak woodland. Therefore, our results may not be representative of conditions in other vineyards in the area. Additional research is needed in the more traditional vineyards, which are typically characterized by large, flat expanses of vines and a lack of large trees.

Adding nest boxes to certain habitats has been found to increase the breeding densities of several species of SCNBs (Brawn and Balda 1988, Newton 1994, Twedt and Henne-Kerr 2001). However, density can be a misleading indicator of habitat quality (Van Horne 1983). Therefore, adding nest boxes to vineyard habitats may enhance those habitats so that they serve as population sources that could stem the decline of Western Bluebirds; conversely, such vineyards could be functioning as "ecological traps" (Delibes et al. 2001, Mänd et al. 2005), population sinks that yield no net reproduction. It is important to note that our survival and productivity results come from a single breeding season and from a minimum-impact vineyard; also, nestling condition and post-fledging survival were not quantified. Additional research investigating post-fledging survival and nest-site fidelity are needed in vineyards with nest boxes to clarify their role as population sources or sinks.

Though our data indicate that vineyards with nest boxes provide suitable breeding habitat for bluebirds, nest boxes in vineyards should not be viewed as a remedy for the chronic problem of habitat degradation and loss of oak woodlands. Møller (1989) and Purcell et al. (1997) also warned against using nest boxes as a cure-all for declining populations. Whereas nest boxes may be an effective, short-term conservation tool for enhancing or maintaining populations of SCNBs—Western Bluebirds in particular—they do not mitigate the effects of chronic habitat loss for the many species that occupy oak woodland habitats in California.

ACKNOWLEDGMENTS

We thank three anonymous reviewers for their invaluable comments on this manuscript. We thank A. Prevel and K. Vincent for their help erecting and monitoring nest boxes in 2003; M. Battany for assistance with the dataloggers; D. Tempel, D. Winslow, S. Bremner-Harrison, and B. Cypher for comments on the manuscript; and D. Filiponi and D. John for allowing us access to the Santa Margarita Ranch and for logistical support in and around the Cuesta Ridge Vineyard. The University of California (UC) Integrated Hardwood Range Management Program Grant # 00-4 supported this research; the Morro Coast and the Santa Barbara Audubon societies provided supplemental funding. The UC Cooperative Extension Office, San Luis Obispo, provided logistical support.

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The Wilson Journal of Ornithology 118(4):558–562, 2006

SEXUAL DIMORPHISM, DISPERSAL PATTERNS, AND BREEDING BIOLOGY OF THE TAIWAN YUHINA: A JOINT-NESTING PASSERINE

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ABSTRACT.—We studied the breeding ecology of Taiwan Yuhinas (*Yuhina brunneiceps*) at the Highlands Experiment Farm at Meifeng, National Taiwan University, in 1995 and from 1997–2002. The Taiwan Yuhina is a joint-nesting, cooperatively breeding species endemic to Taiwan. Males had significantly longer wing chords and tail lengths than females, probably due to sexual selection. Males also had a longer residence time at Meifeng than their female mates, which could be explained by philopatry being greater in males. Alpha males had a significantly longer residence time at Meifeng than beta males, but this was not the case for females, because females did not remain in the same group as males did after their mates disappeared. The breeding season was approximately 6 months long and multiple brooding was common. Nest building took 3 days, egg laying occurred over 3–4 days, the average incubation period was 14 days, and the nestling period was 12 days. Breeding success did not decrease later in the breeding season. Maximum longevity was 12 years, and the estimate of average annual overwinter survival rate for adults at Meifeng was 74%. *Received 3 August 2005, accepted 3 May 2006.*

The Taiwan Yuhina (*Yuhina brunneiceps*), a Timaliine babbler, is a resident bird species endemic to subtropical Taiwan (Clements 2000). Male and female yuhinas are morphologically indistinguishable in the field. Joint-nesting behavior in yuhinas was first described by Yamashina (1938). Recently our group reported the social system (including joint nesting) and reproductive success (Yuan et al. 2004), incubation behavior (Yuan et al. 2004, 2005), and habitat selection (Lee et al. 2005) of yuhinas from a 7-year intensive study. Yuhinas formed breeding groups of 2–7 individuals; group-size mode was four. The yuhina is the only known passerine species to adopt a joint-nesting strategy for a large proportion of its nests (Vehrencamp and Quinn 2004).

The majority (69%) of passerine species have been considered sexually monomorphic (Barraclough and Harvey 1995); however, for many avian species there are subtle sexual differences in plumage color and morphology (Mays et al. 2006). Animals that live in groups usually establish hierarchies, and members of different hierarchical levels often differ in terms of body size and age. Therefore, morphological and age comparisons between individuals of different sexes and hierarchical levels will shed light on the extent of sexual selection and the process of group formation. In this paper we describe the morphological differences between male and female yuhinas, residence times of different sexes and hierarchies, breeding chronology, longevity, and adult survival rate.

METHODS

We studied a population of yuhinas at the Highlands Experiment Farm at Meifeng, National Taiwan University, in central Taiwan (24° 05′ N, 121° 10′ E; 2,150-m elevation) during 1995 and from 1997–2002. The study area is described in detail elsewhere (Yuan et al. 2004).

During this study, we color-banded 252 adult yuhinas. We measured bill, head (from the back of the cranium to the upper bill tip), tarsus, relaxed wing chord, flattened wing chord, and tail length; crest height (from the base of the bill to the tip of the longest crest feather) and width (above the eyes); and the weight of each captured adult. A 20- to 70-μL blood sample was collected from the brachial vein of each adult and juvenile. Each sample was transferred into 500-μL Queen's lysis buffer (Seutin et al. 1991) and frozen at

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−20°C until analyzed. Sex was tentatively assigned in the field based on observations of singing and copulation and later verified using sex-specific genetic markers (Fridolfsson and Ellegren 1999).

We defined a breeding group as a set of individuals exhibiting parental behavior toward the young of a single nest. Within each group, there was a linear hierarchy of socially monogamous pairs. Dominance hierarchies were easily determined by observing chasing and displacement behavior among group members (Yuan et al. 2004). We monitored the breeding chronology of 4, 6, 10, 11, and 13 groups in 1997, 1998, 1999, 2000, and 2001, respectively. Mayfield nest survival rates (Mayfield 1961, 1975) for different months were ascertained by intensively monitoring 13 breeding groups in 2001. Nest status was checked at 2- to 10-day intervals in different years. Predation events were determined by checking whether there were eggs, remains of eggs, or nestlings left in the nest. We assumed that there was no partial predation at yuhina nests, which was reasonable because the eggs and nestlings are rather small compared to those of their predators. We confirmed this assumption later by video-monitoring nests.

To estimate the adult overwinter survival rate, we monitored the fate of 125 banded individuals. For the years 1997–1998, 1998–1999, 1999–2000 and 2000–2001, we divided the number of banded birds that survived to the second year by the number of banded birds present in the first year. Following Vehrencamp et al. (1988), we identified six categories of disappearance: one of a mated pair; a dominant mated pair; an unmated bird; a non-breeding bird; a bird of uncertain status; and an entire group. We only counted the first two categories as mortalities; the others were more likely to have dispersed.

In 1990, 10 adult yuhinas were banded at Meifeng as part of a previous study (C.-W. Yen pers. comm.). Recaptures of these birds were used to estimate long-term survival. Because most birds were banded as adults, we could not determine their exact ages. Instead, we calculated minimum residence time at Meifeng. For banded birds present in 2000 and 2001, we determined the number of years in residence from the date of banding. Birds present in both years were counted only once (in 2001).

Statistical analyses were performed using SAS software, ver. 8 (SAS Institute, Inc. 2000). The morphological characteristics and residence times of mated males versus females, and of alpha versus beta males and alpha versus beta females, were compared using unpaired or paired (as appropriate) t-tests to determine whether there were significant differences between groups. Means are represented as ± SD.

RESULTS

The behavior of 118 individuals was observed in the field and their sexes were determined by genetic markers. We correctly identified the sex of all paired individuals in the field, including 53 males and 47 females. However, the sex of unpaired individuals was difficult to determine solely by field observation. Of 18 unpaired birds, including 10 males and 8 females, the sex of only 6 males (and no females) was successfully determined by behavioral observation. Wing chord and tail length of males were significantly greater than those of females, but we detected no statistically significant differences in any other morphological variables (Table 1). Males also had a longer residence time than their mates (3.2 ± 2.2 versus 2.4 ± 1.7 years; paired t-test: $t_{16} = 2.36$, $P = 0.033$). In addition, we found that, for a given group, alpha males had longer residence times than beta males (4.3 ± 1.7 versus 2.8 ± 1.3 years; paired t-test, $t_{12} = 2.92$, $P = 0.014$). We found no difference in residence times of alpha versus beta females (3.2 ± 1.9 versus 2.5 ± 1.1 years; paired t-test, $t_{11} = 1.10$, $P = 0.30$).

The breeding season lasted approximately 6 months, beginning in March or April and ending in August or September. Weather and predation were the two major causes of nest failure. In 2000 and 2001, strong winds and heavy rains during typhoons and afternoon thunderstorms destroyed 58% ($n = 12$) and 21% ($n = 42$) of the nests, respectively. Predators caused the failure of 21% (2000) and 55% (2001) of nests. Confirmed predators of yuhina eggs and nestlings were Eurasian Jay (*Garrulus glandarius*) and Taiwan Sibia (*Heterophasia auricularis*).

Nest success did not decrease as the season

TABLE 1. Morphological measurements (mm, except for weight) of male and female Taiwan Yuhinas from 17 groups studied in 1995 and from 1997–2001 in Meifeng, Taiwan (24° 05′ N, 121° 10′ E). Significant between-gender differences are boldfaced.

	Male	Female		
Measurement	Mean ± SD (*n*)	Mean ± SD (*n*)	*t*	*P*
Bill	11.9 ± 0.3 (25)	11.9 ± 0.6 (28)	0.19	0.85
Head	29.7 ± 0.6 (30)	29.6 ± 1.3 (27)	−0.29	0.78
Tarsus	17.9 ± 0.6 (25)	17.8 ± 0.6 (28)	0.81	0.42
Wing chord				
Relaxed	62.0 ± 1.6 (27)	59.9 ± 1.4 (31)	5.26	**<0.001**
Flattened	63.5 ± 1.6 (26)	61.9 ± 1.6 (31)	3.86	**<0.001**
Crest height	27.4 ± 1.5 (13)	26.3 ± 1.2 (13)	1.76	0.10
Crest width	10.7 ± 0.7 (13)	10.6 ± 1.2 (9)	0.22	0.83
Tail	46.3 ± 1.9 (27)	45.3 ± 1.3 (31)	3.20	**<0.001**
Weight (g)	12.5 ± 0.8 (22)	12.3 ± 0.8 (26)	0.98	0.33

progressed in 2001 (linear regression, $F_{1,4} = 0.001$, $P = 0.89$; Fig. 1), and multiple-brooding was common among yuhinas at Meifeng. In 1997, 1998, and 2000, at least 3 of 26 groups successfully raised chicks to fledging in three consecutive broods, and at least 4 groups produced two successful broods each. In 2001, one group made nine nesting attempts after prior attempts were destroyed either by inclement weather or predators. In 2000 and 2001, we found one and two cases, respectively, in which group members were building a new nest while still feeding fledged young from their previous brood. Nest building took approximately 3 days and egg laying occurred over 3–4 days. Incubation averaged 14.3 ± 1.9 days ($n = 21$) and the nestling period was 11.6 ± 2.0 days ($n = 19$). Renesting attempts were usually initiated within 17.5 ± 2.6 days ($n = 7$) of fledging from the first nest if the nest was successful and within 5.8 ± 3.5 days ($n = 49$) if the nest failed.

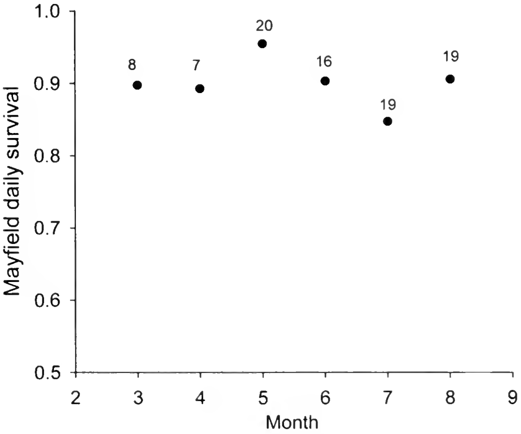

FIG. 1. Mayfield daily survival of Taiwan Yuhinas in different months of 2001 at Meifeng, Taiwan (24° 05′ N, 121° 10′ E). Survival did not decrease later in the breeding season. Sample size (nests) is shown above each point; month number corresponds to month sequence in a calendar year (i.e., 2 = February, 3 = March, etc.).

Of the 10 adult yuhinas banded in 1990, we recaptured four in 1998 (i.e., they were >9 yr old). Only one of the four was seen in 1999, and this individual was seen again in 2001 (>12 yr old). The estimated average annual adult overwinter survival was 74 ± 5% (n = 4 yr and 125 individual-yr).

DISCUSSION

At Meifeng, breeding males had longer residence times than did the females. Alpha males had longer residence times than beta males, but female dominance was not correlated with residence time. The longer residency of alpha males is likely because males need to queue into the groups to become dominants (Kokko and Johnstone 1999). The difference in male and female residence times could be explained by our observation that female status depended on the status of their mates: when paired alpha females disappeared, most of their mates retained their alpha status and found a new mate, but, when paired alpha males disappeared, few of their mates retained their dominant status (Yuan et al. 2004). Females had shorter residence times than their mates, possibly because females dispersed farther and searched for mates in larger areas, which might have increased their chances of encountering available dominant males. Alternatively, females might be forced to disperse when their mates die. Males remained in a group and queued for better breeding status for comparatively longer periods of time. Another explanation for the difference in male and female residence times might be different survival rates between males and females. Additional data on the relationship between age structure and group composition are needed, especially as they relate to sex and dominance.

The size difference between breeding male and female yuhinas could indicate that sexual selection has been occurring in this species. Larger body size is related to a better ability to compete for resources (Pusey and Packer 1997). Indeed, the body size of higher ranking male yuhinas was greater than that of lower-ranking males, but there was no such difference in females (Yuan et al. 2004). Because a female yuhina's status is dependent upon that of her mate, larger males might have an advantage because they can maintain higher breeding status and more easily attract mates.

Given that we did not find any evidence for a seasonal decline in nest success, and because harsh weather and predation were the main causes of nest failure, we reasoned that the combined effects of weather and predation pressure were consistent within a given breeding season. Therefore, the ability to renest faster and more frequently is probably one of the main determinants of the yuhina's seasonal fecundity. As we have shown, yuhinas could make up to nine nesting attempts and were able to fledge multiple broods in a season. This result supports the recent argument that the number of nesting attempts made by songbirds is usually greater than formerly assumed (Farnsworth and Simons 2001, Grzybowski and Pease 2005). A seasonal trend in clutch size could have been another important factor affecting seasonal fecundity of yuhinas (e.g., Winkler and Allen 1996), although we did not have enough data to evaluate this possibility. Because yuhinas are too small to mob most of their predators and can renest faster in larger groups, we suggest that the joint-nesting behavior is a bet-hedging strategy to cope with the yuhina's highly variable environment, such as frequent typhoons and a high risk of predation; yuhinas invest less in single attempts and renest faster to permit more nesting attempts (Yuan et al. 2004).

ACKNOWLEDGMENTS

We thank H. L. Mays, Jr., D. B. Burt, P. F. Coulter, and three anonymous reviewers for valuable comments on an earlier draft of our manuscript. We thank M.-C. Tsai, K.-Z. Lin, and workers at Meifeng Farm for logistical support. We greatly appreciate the volunteers from the National Taiwan University Nature Conservation Students' Club and School of Forestry and Resource Conservation, in particular M. Liu, I.-H. Chang, and K.-D. Zhong for their help in the field and lab. Our research was supported by grants from the National Science Council, Taiwan.

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Short Communications

The Wilson Journal of Ornithology 118(4):563–566, 2006

Ant Presence in Acacias: An Association That Maximizes Nesting Success in Birds?

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ABSTRACT.—Nest predation is the main cause of reproductive failure in birds, yet the factors that drive predation pressure, as well as the avian strategies to minimize it, are poorly understood. There is a well-known commensal relationship between ants and birds nesting in acacia trees, but the direct benefit in terms of avian reproductive success has not been tested properly. We used artificial nests to compare success and survival probability of nests placed in Hinds' acacia trees (*Acacia hindsii*) associated with ants (*Pseudomyrmex* spp.) with those of nests placed in trees without ants. Nesting success and the probability of daily survival were greater in acacias than in antless trees. All cases of nest failure were due to egg predation, but none resulted from wren activities, as has been reported in previous studies. The results of this experimental study indicate that the presence of ants in acacias may enhance avian reproductive success by reducing the probability of nest predation. *Received 30 June 2005, accepted 28 June 2006.*

Several bird species of the families Formicariidae, Tyrannidae, Troglodytidae, and Emberizidae prefer to establish their nests in acacias with which *Pseudomyrmex* spp. ants associate (Janzen 1969, Young et al. 1990, Flaspohler and Laska 1994). The relationship between birds nesting in acacias inhabited by ants seems to be commensal, because ants that protect acacias against herbivores also offer protection against avian nest predators (Skutch 1945, Janzen 1983, Flaspohler and Laska 1994). On the other hand, birds do not seem to provide any benefit to acacias or ants (Gilardi and Von Kugelgen 1991).

It has not been proven, however, that a myrmecophytic association confers greater breeding success to birds. A study conducted in Costa Rica (Young et al. 1990) revealed a 36% failure rate of artificial nests (n = 50) placed in myrmecophyte acacias, but, in antless tress, only 18% (n = 49) of the nests failed (Young et al. 1990). Of the failed nests, 72% of those located in acacias and 44% of those located in antless trees failed due to egg destruction by Rufous-naped Wrens (*Campylorhynchus rufinucha*).

We conducted an experiment on the Pacific coast of Mexico using artificial nests to determine whether the myrmecophytic association confers a benefit to birds in terms of greater nesting success. We also examined whether nesting failure at our study site was related to egg destruction by species ecologically equivalent to the Rufous-naped Wren (Ehrlich et al. 1988, Dion et al. 2000)—Sinaloa Wren (*Thryothorus sinaloa*), Happy Wren (*T. felix*), and White-bellied Wren (*Uropsila leucogastra*).

METHODS

We conducted our study during September 2004 in the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Mexico (19° 30′ N, 105° 0.3′ W). Tropical dry deciduous forest is the dominant vegetation, and acacias generally occur as secondary growth in locally distributed sites near the coast. We collected data at two sites characterized by similar vegetation: Careyes and Negritos, situated southeast and northeast, respectively, of the Biological Station. We randomly selected a 1-km transect at each site and placed 28 artificial nests along each transect: 14 in Hinds' acacia trees (*Acacia hindsii*) and 14 in antless trees. The cup-shaped nests were placed 1.7–2.2 m above ground and wired to the tree trunks. In each nest, we placed three hand-made eggs (20-mm length)—made of white plasticine and sprayed with varnish—to resemble eggs

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of the Social Flycatcher (*Myiozetetes similis*). Social Flycatchers are common breeders in the area and reportedly nest in acacias (Pettingill 1942). Predators readily left marks in the plasticine, thus allowing us to identify predator species and the impact of wrens on nesting success, if any (Major 1991, Major and Kendal 1996, Dion et al. 2000, Zanette and Jenkins 2000).

Nests were exposed to predators for 6 days. We recorded egg condition every 2 days and removed those nests in which eggs showed evidence of predation. Based on previous reports (Kennedy and White 1996, Hannon and Cotterill 1998), wren species usually peck small holes in the eggs of other species. To determine whether wrens were responsible for nest "failure," we compared marks on the plasticine eggs recovered from depredated nests with those we made using the bills of museum specimens representing the three wren species that occurred in our study area: Sinaloa Wren, Happy Wren, and White-bellied Wren.

The percentage of nests in which no eggs showed damage by the end of our experiment was our measure of nesting success. To determine differences in failure probabilities between sites and tree type in which nests were located, we analyzed the data with a linear generalized model (GENMOD), assuming a binominal distribution and a logit function (SAS Institute, Inc. 2000). The independent categorical variables were our two sites (Careyes and Negritos) and the two tree types (myrmecophyte acacia or antless tree); in both cases the dependent variable was the probability of nest failure.

We calculated daily survival rate (DSR), by tree type, using the daily probability of nest survival. Survival rate—the most reliable measure of nesting success (Ralph et al. 1996)—was calculated with the MAYFIELD program (Hines 1996) based on the method proposed by Mayfield (1961, 1975) and revised by Bart and Robson (1982). Differences in DSR means were assessed with a *Z*-test using variances obtained from the MAYFIELD program. Means are reported ± SE.

RESULTS

Nest success was similar at both sites (39% at Careyes and 43% at Negritos; $\chi^2 = 0.15$, $P = 0.70$, df = 1). However, nest success was greater for nests placed in acacias (64.3%) than those placed in antless trees (17.8%; $\chi^2 = 13.06$, $P < 0.001$, df = 1). Because there was no site effect, we pooled our data for calculating DSR estimates. DSR was greater for nests located in acacias (0.944 ± 0.017, $n = 28$) than it was for those located in antless trees (0.808 ± 0.036, $n = 28$; $Z = 10.73$, $P = 0.010$). Overall nest survival (6 days of exposure) was 70.5% ($n = 28$) in acacias, and 28% ($n = 28$) in antless trees. All nest failures were due to predation; however, based on our observations of marks left on the plasticine eggs, no eggs were destroyed by wrens.

DISCUSSION

Our results indicate that the type of tree where nests were placed (acacias versus antless) affected the probability of nest success. Probability of survival was greater for nests placed in acacias, which may be related to the presence of ants. This supports Skutch's (1945) hypothesis, which suggests that nests in acacias have a higher probability of survival due to the ants that associate with them, despite the minimal cover that acacias provide for nest concealment (Young et al. 1990). The results of previous studies with artificial nests of other species indicate that egg predation may be greater where canopy cover is minimal (Crabtree et al. 1989, Sullivan and Dinsmore 1990, Mankin and Warnen 1992, Martin 1992; but see Gottfried and Thompson 1978). Although we did not measure canopy cover around the nests, egg predation was not greater under the poor canopy cover that characterizes *Acacia* spp. Indeed, low rates of egg predation in acacias—despite their minimal foliage cover—underscores the potential role of ants in providing protection against nest predators.

In Costa Rica, the success rate of artificial nests placed in acacias (64%; Young et al. 1990) was similar to the rate we detected at Chamela (64.3%), but the percentage of successful nests in antless trees was much greater (81.6%) than it was at Chamela (17.8%). In addition, we found no evidence of wren predation on eggs, though longer observation periods may be necessary to confirm this pattern. The low rates of success that we observed for nests placed in antless trees (entirely due to predation) suggest that, in the absence of Rufous-naped Wrens, acacias with which ants associate increases the probability of avian nest survival, despite of the presence of other wren species.

Previous researchers have proposed that birds reduce the probability of nesting failure by minimizing parental activity around the nest (Martin et al. 2000); producing smaller clutches to minimize parental activity (Skutch 1949, 1976) or to save energy for a second brood (Slagsvold 1982); evolving shorter incubation periods (Ricklefs 1969; but see Martin 2002); and/or nesting at the end of the dry season (Morton 1971, Poulin et al. 1992). Janzen (1969) and Young et al. (1990) found that several species were more likely to nest in acacias than in antless trees. Consistent with these observations, our results indicate that artificial nests located in acacias with ants have greater probabilities of nest survival. Thus, we propose that this may be yet another strategy for maximizing nest success.

Unfortunately, no antless acacias were available at our study sites; evaluations of nest success in antless acacias will be necessary to confirm the role of ants in discouraging predation. In addition, evaluating the effects of different acacia species, canopy cover, and the possible influence of different ant species on nest success will provide better insights into the mechanisms behind enhanced nesting success in acacias with which ants associate.

ACKNOWLEDGMENTS

M. Quesada, I. Herrerías, P. Cuevas, and G. Sánchez supported the planning and development of our project. K. Renton provided material and ideas for developing the study. B. Milá, F. López, C. González and two anonymous reviewers provided comments that improved the manuscript. We thank P. Mosig and E. Silva for helping us with manuscript translation. Estación de Biología Chamela of the Chamela-Cuixmala Biosphere Reserve provided field facilities.

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The Wilson Journal of Ornithology 118(4):566–569, 2006

Pair Roosting of Nesting Carolina Wrens (*Thryothorus ludovicianus*)

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ABSTRACT.—Carolina Wrens (*Thryothorus ludovicianus*), which maintain lifetime pair bonds and year-round territories, huddle in pair or communal roosts during the non-breeding season, particularly during cold winter nights. Pair roosting during the nesting season, however, is not known to occur. Here, we report huddled pair roosting by Carolina Wrens in Florida. The dates of pair roosting took place during nest construction through laying of the first egg (9–20 March 2004), and also on the date the fourth egg was laid in a clutch of five (24 March). The wrens roosted in a hanging flower basket located 2.4 m from their nest site. Although huddled pair roosting by wrens during periods of low ambient temperatures in the non-breeding season likely achieves thermal conservation, the benefits derived during the breeding season remain unclear. We discuss the possible thermoregulatory and pair-bond maintenance functions of pair roosting. *Received 6 September 2005, accepted 5 July 2006.*

Roosting by two or more birds has been hypothesized to ameliorate the energetic cost of thermoregulation during cold temperatures, lower the risk of predation, and improve foraging efficiency (Beauchamp 1999). Numerous researchers have examined pair, communal, or huddled roosting during the non-breeding season (in cavities: du Plessis and Williams 1994; in dormitory nests: Sharrock 1980, Gill and Stutchbury 2005; in foliage: Balda et al. 1977). Yet, the occurrence and function of these types of roosts during the breeding season remains a poorly understood aspect of avian behavior.

The Carolina Wren (*Thryothorus ludovicianus*) is the only *Thryothorus* wren whose range extends beyond tropical latitudes (Morton 1982). In contrast to wren species with which it is sympatric in North America, Carolina Wrens form lifetime pair bonds and defend a territory throughout the year (Morton and Shalter 1977). They also roost in a variety of natural and anthropogenic structures (Haggerty and Morton 1995) and are known to roost in pairs during the non-breeding season (Brooks 1932, Tamar 1980). Whereas some tropical wrens form communal or pair roosts throughout the year (Skutch 1940, Robinson et al. 2000, Gill and Stutchbury 2005), to our knowledge there are no reports of pair roosting during the breeding season for tropical or temperate populations of Carolina Wrens. Laskey (1948) assumed that both members of a

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pair of Carolina Wrens she observed during the egg-laying phase were roosting together, but she did not confirm this. Here, we confirm huddled pair roosting by Carolina Wrens during the egg-laying phase of the nesting season in northern Florida.

Observations were made in an urban setting (residence of RFL) in Gainesville, Florida (29° 40′ N, 82° 24′ W). From 5 to 17 March 2004, a pair of Carolina Wrens carried nest material to the base of a potted bromeliad on an east-facing ledge, 1.2 m above the floor of a covered patio deck. On 9 March, approximately 5 min after sunset, the pair flew directly to the rim of an open-topped hanging plant basket (devoid of plants) 2.4 m from the nest site and, within seconds, dropped down to roost in the slightly cupped depression on the peat/soil surface. From 10–15 March, the pair exhibited similar roosting behavior, both birds arriving at the roost site at the same time. On 16 March, just after sunset, one of the pair went to roost in the hanging basket, and emitted soft "cheeps" until the second wren joined it 4 min later. This roosting pattern was repeated in a similar fashion from 17–19 March.

The first egg was deposited in the nest shortly after sunrise on 20 March and, on this date, the pair again roosted together. On 21 and 22 March, the second and third eggs were laid, and one bird (presumably the female) roosted on the nest while the other roosted in the hanging basket. On 23 March, however, when the fourth egg was laid, both wrens roosted in the hanging basket. This date was the last on which both birds were observed roosting together. On 24 March, when the fifth and final egg of the clutch was laid, one bird roosted on the nest and the other in the hanging basket. On 25 March, only the bird roosting on the nest was observed; however, on the following night, one of the pair roosted in the hanging basket and the other on the nest. After 26 March, no further roosting in the hanging basket was observed.

This pair of Carolina Wrens roosted together in the hanging basket for a period of 12 days (9–20 March), which spanned the period of nest construction and deposition of the first egg. They roosted together again only on 23 March, the day on which the female laid the fourth egg of the five-egg clutch. Observations on 4 of the 13 nights during which the pair roosted together revealed that the two birds were always in contact with one another (huddled), with one wren positioned slightly in front of the other. The roosting birds always departed from the roost site shortly after daybreak. The eggs hatched on 9 April, and four young fledged on 18 April with both adults present.

We discuss two alternative, but not mutually exclusive, explanations for these observations: thermoregulation (Beauchamp 1999) and pair-bond maintenance (Kellam 2003). Small birds lose heat rapidly, even in tropical climates (Merola-Zwartjes 1998), and the energetic cost of thermoregulation is high (Ferguson et al. 2002). At low ambient temperatures in winter, Carolina Wrens in the temperate region can experience high mortality (Brooks 1936, Tamar 1980). A possible negative relationship between temperature and diurnal foraging time for Carolina Wrens (Strain and Mumme 1988) could further limit the energy available for nocturnal thermoregulation. Given that low temperatures increase the energetic requirements of birds, and that the energetic requirements of female birds increase before and during laying (Nager and van Noordwijk 1992), a laying female may display behaviors that would mitigate thermoregulatory losses resulting from low nocturnal ambient temperatures (Weeks 1994). Pair roosting by altricial passerines may create a microclimate that ameliorates the energetic costs of thermoregulation (Merola-Zwartjes 1998) and mitigates the effects of low temperature on decreased egg volume (Nager and van Noordwijk 1992) and on interrupted egg laying (Yom-Tov and Wright 1993).

Nocturnal temperatures during the period (5–26 March) of our observations generally ranged between 7 and 10° C (http://weather.herald.com/auto/miamiherald/history/airport/KGNV/2004/3/26/DailyHistory.html). Minimum temperatures during the nights when the pair roosted together averaged 2° C colder than the other nights during March 2004. The wrens roosted together on 8 of the 10 coldest nights of the month, and only on 1 of the 10 warmest nights of the month. The roosting birds fluffed their head, back, and rump feathers—typical of sleeping wrens (Williams 1941, Haggerty and Morton 1995). Feather erection not only facilitates convective cooling of birds in hot climates (Ferns 1992), but also reduces the thermal conductance of plumage, thus providing insulation (Ferguson et al. 2002) in cold climates. If thermoregulation best explains pair roosting by Carolina Wrens during egg laying, both parents may benefit via enhanced egg volume and uninterrupted laying. However, if roosting in cavities and roost nests evolved as an anti-predator behavior (Merola-Zwartjes 1998), any thermoregulatory benefit might be only coincidental.

Pair roosting before and during egg laying may reinforce the pair bond and prevent divorce in Carolina Wrens. Behaviors that promote contact, achieve breeding synchrony, and demonstrate commitment may serve to maintain avian pair bonds (Hall 2000). For example, some males of a tropical congener species that forms permanent pair bonds may initiate duets in order to limit extra-pair mating and divorce (Gill and Stutchbury 2005), and, in some passerine species that form lifetime pair bonds, both sexes may actively guard their mates (Hall 2000, Gill 2003). Carolina Wrens are genetically monogamous and rarely divorce (Haggerty et al. 2001); thus, we might expect at least one sex to actively limit extra-pair mating. Due to the rigors of fledgling care and providing food to their mates, Haggerty et al. (2001) doubted that male Carolina Wrens could prevent females from engaging in extra-pair mating; however, this explanation does not preclude males from mate guarding during the relatively less intense nest-building and egg-laying phases.

Paired female Carolina Wrens may have a higher probability of year-round survival than solitary females (Haggerty et al. 2001). Morton and Shalter (1977) speculated that because individual male Carolina Wrens can maintain a territory, whereas individual females cannot, females may actively reinforce the lifetime pair bond as a safeguard against divorce. Accordingly, the female would likely initiate pair roosting during the nesting season. In our observations, both members of the pair arrived at the roost simultaneously during nest building, but, as laying approached, the birds arrived separately and one bird (sex unknown), called to the other from the roost. Of the Carolina Wren pair that she observed, Laskey (1948) noted that the male arrived first at the roost site and called to the female from there. This anecdotal evidence suggests that pair roosting during nest construction and egg laying is initiated by the male. Because the wren's short period of fertility represents the most advantageous time for opportunistic males to mate with other females (Gill 2003), mate guarding by males during egg laying seems plausible.

In this paper, we have reported huddled pair roosting by Carolina Wrens during the nesting season, and we have discussed two possible mechanisms, thermoregulatory benefits and pair-bond maintenance, to explain this behavior. The possibility that this behavior was that of a non-breeding pair continuing their winter roosting into the early part of the nesting season is most unlikely for two reasons: (1) the pair roosting that we observed spanned the duration of nest construction and egg laying, and (2) other physiological and behavioral changes occur concomitantly during this phase of the breeding season. Consequently, the evidence suggests that we documented a previously unconfirmed behavior. Whereas the functions of huddled pair and communal roosting during the non-breeding season have been studied in detail, more study is needed to identify the function of pair roosting during the breeding season by birds that form lifetime pair-bonds, and which sex, if either, typically initiates pair roosting.

ACKNOWLEDGMENTS

Earlier versions of this manuscript were improved thanks to comments from T. A. Contreras, S. A. Gill, K. E. Sieving, and two anonymous reviewers. This paper is a contribution (Journal Series No. R-11007) of the Florida Agricultural Experiment Station, Gainesville, Florida.

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The Wilson Journal of Ornithology 118(4):569–570, 2006

Bald Eagle Kills Crow Chasing a Hawk

Bruce D. Ostrow[1]

ABSTRACT.—I report predation of an American Crow (*Corvus brachyrhyncos*) by a Bald Eagle (*Haliaeetus leucocephalus*) in Washington state. The crow was attacked and killed while it was chasing a Red-tailed Hawk (*Buteo jamaicensis*). To the best of my knowledge, this is the first report of a bird of one species killing a bird of a second species that was chasing a bird of a third species. *Received 15 September 2005, accepted 5 May 2006.*

On 8 August 2005, along with five other observers, I was observing a mature Bald Eagle (*Haliaeetus leucocephalus*) at Hammersley Inlet (47° 12′ N, 122° 56′ W) near Arcadia in Mason County, Washington, while in a boat drifting in the middle of the narrow inlet. I was using an 8 × 30 monocular to observe the eagle, which was perched in a tree on the southeast side of the inlet, ~100 m away from the boat.

At 15:22 PST, I noticed a Red-tailed Hawk (*Buteo jamaicensis*) and an American Crow (*Corvus brachyrhyncos*) fly out of the trees on the northwest side of the inlet. The crow was chasing the hawk and repeatedly attacking the

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hawk's tail from above with its bill and feet in typical mobbing behavior. The hawk and crow were flying southeast across the inlet directly toward the eagle. When the hawk and crow were halfway across the inlet, ~50 m from my position, the eagle flew directly at the pair. Just as the eagle reached them, the hawk dived out of the way, but the crow did not have time to evade the eagle. The eagle grabbed the crow head-on with its talons, killing it instantly. The hawk flew away quickly to the northeast, and the eagle took the dead crow to the southeast bank below its initial perch. The entire sequence of events occurred in ~10 sec.

Within 1 min of landing, the eagle flew away to the northeast, leaving the crow's carcass on the bank. I was unable to ascertain whether the eagle ate any of the crow because the carcass was hidden from view and the eagle did not return within the time I remained in the area (2 min). I do not believe that the presence of our boat of observers influenced the birds' behaviors. Their flight paths were direct and they were actively engaged with each other. Also, I doubt that our presence scared away the eagle because the boat was drifting silently and was out of sight of the eagle when the bird was on the bank.

Mobbing is a common avian response used to drive away larger predators, including Bald Eagles (Hayward et al. 1977). Mobbing cannot take place without risk, however, as sometimes the mobbing bird (including crows) is killed by the bird it is harassing (reviewed by Sordahl 1990). To the best of my knowledge, this is the first report of a bird of one species killing a bird of a second species that was chasing a bird of a third species. Southern (1970) reported a Northern Harrier (*Circus cyaneus*) chasing away eight crows that were mobbing a Great Horned Owl (*Bubo virginianus*), but none of the crows were harmed. Rudebeck (1951), however, reported a Peregrine Falcon (*Falco peregrinus*) capturing a Northern Lapwing (*Vanellus vanellus*) that had been harassing the author. My observation, along with these other observations, suggests that a mobbing bird may be a relatively easy target for predators, as it is otherwise preoccupied.

ACKNOWLEDGMENTS

I would like to thank M. P. Lombardo, T. A. Sordahl, W. E. Southern, and an anonymous reviewer for critically reading this manuscript. O. M. Ostrow, F. Q. Ostrow, G. L. Sass, R. P. Royal, and A. B. Royal also observed this event.

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The Wilson Journal of Ornithology 118(4):571–572, 2006

Rapid Beak-Swinging Locomotion in the Puerto Rican Spindalis

Ernest H. Williams, Jr.[1,3] and Lucy Bunkley-Williams[2]

ABSTRACT.—We observed a Puerto Rican Spindalis (*Spindalis portoricensis*, Thraupidae) rapidly move through an area of dense vines by grasping vines in its beak and swinging from vine-to-vine without the use of its wings or feet. This behavior appears to be unique in birds. *Received 8 August 2005, accepted 24 April 2006.*

The Puerto Rican Spindalis (*Spindalis portoricensis*, Thraupidae) is a moderate-sized (16.5 cm) tanager endemic to Puerto Rico and its eastern islands. It occurs commonly, but rather sporadically (Bunkley-Williams and Williams 2000), in forests and woodlands at all elevations throughout Puerto Rico (Raffaele 1989, American Ornithologists' Union 1998).

At 10:00 AST on 11 April 2005, EHW observed an adult female Puerto Rican Spindalis on the outskirts of the University of Puerto Rico campus in Mayagüez, Puerto Rico (18° 12.85′ N, 67° 08.35′ W; elevation 37 m). The bird flew into a large grove of trumpet trees (*Cecropia schreberiana*, Cecropiaceae) <3 m away from the observer; because the ground sloped downward steeply towards and into the grove and the bird flew from upslope, the bird entered the trees at a height of approximately 6 m without changing its altitude. It flew into an area (~1.5 × 2 m) of densely-packed (~2–10 cm apart), fine-stemmed (4–7 mm in diameter) pudding vines (*Cissus verticillata*, Vitaceae) hanging from a trumpet tree. The vines were denuded of leaves due to a 2-month-long drought. Without slowing, landing, or hovering, the bird grasped one of the vines in its beak, ceased flying, and its momentum swung it into the dense vines. Then it released the first vine and, dropping a few centimeters, grasped a second vine. The bird repeated this action moving to a third, and then a fourth, vine. In this manner, it passed completely through a 1.5-m-wide area of densely packed vines in less than 4 sec without flapping its wings or using its feet to grasp the vines. Without hesitating or stopping, the bird then flew further into the grove of trees.

Rapid, beak-swinging locomotion apparently has not been described for this species, or for any other species that we have been able to determine. Leck (1972) did not report this behavior while observing Puerto Rican Spindalis in trumpet trees in Puerto Rico, and Isler and Isler (1987) did not note it in any of their tanager accounts. However, Garrido et al. (1997) suggested that very little is known about the behavior of *Spindalis* spp.

The described behavior allowed the bird to move through densely packed vines where wings could not be used for support or locomotion. The bird did not appear to feed on anything within the vines, was not being pursued by a predator, and did not collect any nesting material. The behavior did not appear to be a mechanism of accident avoidance (i.e., crashing into the dense vines), as it was too rapid, smoothly coordinated, and complicated.

Birds will sometimes use their beaks to aid locomotion on land (e.g., Turkey Vultures: Vogel 1950; Red-tailed Tropicbirds and White-tailed Tropicbirds: Lee and Walsh-McGehee 1998). Birds are also able to support their body weight with, and swing from, their beak while grasping onto something with it (e.g., Law 1926, Brazil 2002). Birds that hang from perches (chickadees and titmice, Paridae; cockatoos, Cacatuidae; kinglets, Sylviidae; lories, Loriidae; parrots, Psittacidae) are well known to use their bill as a "third foot" to assist in climbing, but unlike what we observed, it is a relatively slow action (Zeefer and Lindhe Norberg 2002) and the feet are used. Although it has been established that birds may exhibit a rapid, swinging locomotion with the aid of their wings and feet (e.g., Potter 2003), our observation should alert oth-

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ers to look for additional cases of swinging locomotion without use of the wings and feet, in both the Puerto Rican Spindalis and in other species.

ACKNOWLEDGMENTS

We thank G. J. Breckon for identifying vegetation mentioned in this manuscript, and A. R. Lewis for reviewing this note. The comments of three anonymous reviewers also improved the paper.

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The Wilson Journal of Ornithology 118(4):572–573, 2006

American Crow Caches Rabbit Kits

Justin J. Shew[1,2]

ABSTRACT.—For corvids, the decision to cache is a complex behavior likely influenced by many interacting factors. On 8 April 2004, I observed an American Crow (*Corvus brachyrhynchos*) caching eastern cottontail (*Sylvilagus floridanus*) kits taken from a rabbit nest on the Missouri State University campus in Springfield, Missouri. The crow cached at least three kits and flew away with at least one other. Caches were covered with dead leaves and landscape mulch. During the ensuing 3-day period, some caches disappeared, were partially eaten, or were moved to a different nearby location. To my knowledge, this is the first documented case of caching numerous rabbit kits from a single nest, and it is one of the few documented cases of cache-moving by American Crows. *Received 29 July 2005, accepted 24 April 2006.*

Many different factors influence caching behavior in American Crows (*Corvus brachyrhynchos*), including food value, handling time, time of day, perishability, and kleptoparasitism (Cristol 2001). American Crows are known to cache various nuts, prey (invertebrate and vertebrate), eggs, dung, and carrion items for later consumption (Phillips 1978, Conner and Williamson 1984, Kilham 1989, Verbeek and Caffrey 2002). Caches are sometimes covered with debris, substrate, or leaves (Phillips 1978, Conner and Williamson 1984, Kilham 1989).

On 8 April 2004 at approximately 17:00 CST (18° C) while walking across the Missouri State University campus in Springfield, Missouri (37° 11′ N, 93° 16′ W), I observed the caching behavior of an American Crow. I heard animal distress calls, which came from an almost hairless baby mammal that the crow (approximately 20–30 m away) was handling in its bill. Although this bill-manipulation period was short (~5–10 sec), it seemed to injure the animal severely and silence its distress calls. The crow was handling the prey while perched on top of a small concrete sign (~1 m tall, ~25 cm wide) on a campus lawn. I slowly approached the crow to within ~5–8 m, and it dropped to the

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ground, quickly picked up surrounding dead leaves and sticks, and placed them over the prey item (cache #1). I uncovered the cache and determined that the mammal was a rabbit kit. I recovered the cache, leaving it in its original location, and continued to watch the crow from approximately 30–40 m away.

The crow flew ~20 m and attended a kit apparently cached earlier (cache #2) in a mulch pile under a landscape tree. The crow then moved this cache to another mulch pile about 5–10 m away, where it carefully picked up individual pieces of mulch and laid them over the cache. Subsequently, the crow pecked around within 0–2 m of the cache while picking up other bits of mulch and quickly dropping them. The crow then flew back to the concrete sign, probed into the ground with its bill, and pulled out an eastern cottontail (*Sylvilagus floridanus*) from a rabbit nest. From there, the crow flew a few meters as the kit gave distress calls; once the kit became silent, the crow cached it (cache #3) in another mulch pile by covering it with mulch and debris. Soon the crow flew back to the cottontail nest, pulled out another kit, and flew northwest beyond my view. After a few minutes, a crow flew from the southwest to the rabbit nest, pulled out another kit, and flew off in the same direction as before.

After another few minutes had passed, a crow flew to the rabbit nest again and probed the nest several times, pulling out only nesting material (dead grass). From there, it went to the first kit (cache #1), uncovered it, and began tearing up and eating the prey. At approximately 17:20, this crow flew away and no crows returned for ~5 min. I then confirmed the locations of caches #2 and #3, finding that kits in both caches were still alive and thoroughly covered with mulch. I also searched other mulch piles in the area, but found no other caches. At 18:45 the same day, the two caches were still in the same locations.

On 9 April at 11:00, I returned to the site to verify the locations of caches #2 and #3. The kits in caches #3 (closest to the cottontail nest) and #2 were gone. I scanned other nearby mulch piles and found a cached kit with a majority of its posterior missing. This half-eaten cache was 5–10 m away from cache #2. At 14:00, the half-eaten kit was in the same location, but on 11 April, the kit remains were gone.

To my knowledge, this is the first observation of an American Crow caching eastern cottontail kits and one of the few documented observations of a cache being stored at multiple locations (cache #2). The kits were 10 cm long and may have represented valuable prey items for a crow, particularly given the cottontail litter size of four to five kits (Whitaker 1996). Similar sightings have entailed a crow in Florida that moved a cached snake (Kilham 1989) and a crow in Tennessee that cached four live gizzard shad (*Dorosoma cepedianum*) in beach sand (Phillips 1978). Also similar to my observations was that of crows on a Texas university campus caching pecans and then tearing up the nearby grass after hiding the caches (Conner and Williamson 1984). The purpose of these post-caching behaviors remains unclear; possibilities include creation of landmarks that help individuals locate their caches, or it may serve to disguise caching behavior from potential kleptoparasites. My observation illustrates some of the complexities of crow behavior, and indicates that more field studies are needed to determine factors that lead to and affect caching behavior.

ACKNOWLEDGMENTS

I thank C. M. Smith for encouraging submission of this short communication and three anonymous referees whose comments improved the manuscript.

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The Wilson Journal of Ornithology 118(4):574–576, 2006

First Nesting Record of the Gray-crowned Yellowthroat (*Geothlypis poliocephala*) in the United States since 1894

Stephan Lorenz,[1,4] Chris Butler,[2] and Jimmy Paz[3]

ABSTRACT.—A Gray-crowned Yellowthroat (*Geothlypis poliocephala*) nest was discovered in Texas during June 2005, providing the first documentation of nesting in the United States since 1894. The nest was located within the Sabal Palm Grove Audubon Center and Sanctuary in Cameron County, but was depredated within 4 days of discovery. Gray-crowned Yellowthroats are fairly common breeders in northeastern Mexico, but are currently listed as accidental in Texas. The future of this species in the United States is uncertain. *Received 7 November 2005, accepted 22 April 2006.*

The Gray-crowned Yellowthroat (*Geothlypis poliocephala*) is a resident species ranging from central Sinaloa and south-central Tamaulipas, Mexico, to western Panama (American Ornithologists' Union 1998). It is found in open, grassy habitats, often with scattered bushes and scrub (Howell and Webb 1995). Before the turn of the 19th century, it was a fairly common breeding species in extreme southern Texas, including Cameron and Hidalgo counties (Oberholser 1974, American Ornithologists' Union 1998). From May 1890 through May 1894, for example, at least 34 specimens were collected near Brownsville, Texas (Lockwood and Freeman 2004), and the population may have persisted into the late 1920s (Lockwood and Freeman 2004).

Currently, the species is listed as accidental in Texas (Bryan et al. 2003), as the last documented breeding record in the United States dates back to 1894 in Cameron County, Texas (Oberholser 1974). Since then, however, the species has been reported from Cameron and Hidalgo counties with increasing frequency. Oberholser (1974) listed records from 1956, 1959, and 1965; more recently, Kutac (1998) and Lockwood (2000, 2001, 2005) listed records from 1988, 1989, 1999, 2000 and 2005. In 1997, a possible breeding pair of Gray-crowned Yellowthroats was found in Webb County, Texas (Woodin et al. 1998). Despite recent sightings of singing males, however, breeding had not been confirmed (Brush 2005).

The reasons for the species' disappearance from Texas are unclear. Habitat similar to that currently occupied by breeding Gray-crowned Yellowthroats in Mexico and Central America is still available in the Lower Rio Grande Valley (Brush 2005). Oberholser (1974) cites habitat reduction caused by development, shifts in agricultural practices, and disappearance of large freshwater marshes as possible reasons for the species' range contraction. Sabal Palm Grove Audubon Center and Sanctuary in Cameron County, Texas (21° 51′ N, 97° 25′ W), is a 213-ha preserve along the Rio Grande that protects one of the last remaining stands of Rio Grande palmettos (*Sabal mexicana*). The site provides habitat for a variety of bird species at the northern terminus of their ranges in the Lower Rio Grande Valley of Texas.

From 8 February (Lockwood 2004) through August 2004 (pers. obs.), a male Gray-crowned Yellowthroat was frequently observed at the Sabal Palm Sanctuary. After August, the bird apparently left the area, but returned on 8 December 2004 (Lockwood et al. 2005) and remained at the sanctuary at least through July 2005 (pers. obs.). On the evening of 25 June 2005, a Gray-crowned Yellowthroat was heard singing at the sanctuary and, the next morning, a Gray-crowned Yellowthroat (presumably the male) was observed carrying food items to a nest hidden in dense grass. Another bird (presumably the female) was flushed from the nest when an observer

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FIG. 1. Male Gray-crowned Yellowthroat (*Geothlypis poliocephala*) captured in a mist net at Sabal Palm Sanctuary in Cameron County, Texas, 29 June 2005 (photograph by C. Butler).

approached the nest site. Later, a Gray-crowned Yellowthroat was again flushed from the nest, after which it gave sharp chips from nearby. On the same date, both birds were observed repeatedly carrying food items to the nest. During 5 hr of observation, the male sang continuously while foraging, primarily near ground level or in dense understory. The song, a musical warble without a clear pattern, was reminiscent of a bunting (*Passerina* spp.) song and decidedly different from that of a Common Yellowthroat (*Geothlypis trichas*). The second bird was observed less often, probably because it was on the nest.

At one point, extended study of the birds' field marks was possible when both birds landed near the grass clump that concealed the nest. Both were medium-sized warblers, larger and bulkier than Common Yellowthroats and with longer tails. Their culmens were curved and their lower mandibles were flesh-colored (Fig. 1). The birds' upper sides were an even, greenish-olive, the wings lacked any patterning or wing bars, and the crowns and auriculars were washed with a slate-gray. Their under parts were predominantly yellow, brightest in the throat area and faded along the flanks, and their bellies were whitish. Observers also noted that the birds had broken eye rings and black lores, the black extending slightly onto the face and creating a black smudge. Gray-crowned Yellowthroats exhibit only limited age- or sex-related plumage dimorphism (Sibley 2000) and the only variation noticed between the two birds was the amount of black extending from the lores onto the face. The presumed male had slightly more black extending up and above the eye, obscuring half of the upper eye-ring arc.

The birds' nest was located along the edge of a dry mesquite (*Prosopis glandulosa*) grassland near a tree-lined resaca. It was 0.3 m above ground on the base of a dense clump of grass (*Panicum* sp.) and constructed mainly of grasses, which is consistent with published descriptions of the species' nesting habits (Oberholser 1974, Howell and Webb 1995, Dunn and Garrett 1997, Martinez et al. 2004). Baicich and Harrison (1997) describe the species' nest as a stout cup of dry grasses and dead leaves built atop a grass tussock. When discovered, the Sabal Palm Sanctuary nest contained four recently hatched nestlings, representing a clutch size typical for Gray-crowned Yellowthroats (3–5 eggs, usually 4; Oberholser 1974, Baicich and Harrison 1997). The hatchlings had blackish down on top of their heads and their eyes were still closed.

On 29 June, a Gray-crowned Yellowthroat was inadvertently caught in a mist net set up as part of an ongoing study on the population biology of "Brownsville" Common Yellowthroats (*Geothlypis trichas insperata*) and located approximately 10 m from the Gray-crowned Yellowthroat nest found at Sabal Palm Sanctuary. The bird was identified as a male, based on a pronounced cloacal protuberance and more extensive black on the lores, and was believed to be the male of the nesting pair (Fig. 1). The plumage characteristics were consistent with those of an after-hatch-year bird. Wing length was 56 mm and mass was 12.9 g, both somewhat greater than the mean wing length (53.6 ± 0.5 SE, $n = 9$) and mean mass (10.6 ± 0.3 SE, $n = 9$) of "Brownsville" Common Yellowthroats ($n = 9$; CB unpubl. data).

On the morning of 30 June, the nest was checked again, but apparently it had been depredated, as all nestlings were gone. The nest was intact, but identification of the predator species would be purely speculative.

Identifying Gray-crowned Yellowthroats in the Rio Grande Valley is difficult due to the possible occurrences of Gray-crowned × Common Yellowthroat hybrids. A male bird present at San Ygnacio in Zapata County, Texas, from 1995 through 1996 was apparently a hybrid, and he paired with a female Common Yellowthroat (Dunn and Garrett 1997). On several visits to the Sabal Palm Sanctuary in March and April 2005, Common Yellowthroats had been observed within the area used by the pair of Gray-crowned Yellowthroats; however, no interactions between the two species were observed. Although we cannot completely rule out the possibility that either of the Gray-crowned Yellowthroats at Sabal Palm Sanctuary was a hybrid, the field marks and song indicated that both birds were "pure" Gray-crowned Yellowthroats.

This documents the first Gray-crowned Yellowthroat nest detected in the United States since 1894. The current breeding site deserves careful monitoring to determine the species' residency status and prevent human disturbance. Prescribed burns in suitable areas (Oberholser 1974), along with further habitat acquisition and protection, could facilitate the return of a breeding population to the United States.

ACKNOWLEDGMENTS

We thank C. Cavazos for assisting in the nest search and T. Brush and J. C. Arvin for their correspondence. We would also like to thank D. W. Pogue, M. W. Lockwood, and R. L. Gutberlet for their help with this manuscript. Additionally, we thank C. E. Shackelford and two anonymous reviewers, who provided helpful comments.

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The Wilson Journal of Ornithology 118(4):577–579, 2006

Once Upon a Time in American Ornithology

Samuel Hearne (Fig. 1) was born in London, England, in 1745. In 1766 he joined the Hudson's Bay Company as a seaman and mate of the *Charlotte*, sailing out of Churchill on Hudson Bay, Canada. In 1771 he was the first European to reach the Arctic coast of North America, traveling on foot with a group of Chipewyan Indians from Churchill to the mouth of the Coppermine River. In 1774 he founded the first inland trading post of the Hudson's Bay Company at Cumberland House, now Saskatchewan's oldest settlement.

Ironically, only the historians appear to have appreciated what a great naturalist Hearne was. In his introduction to the 1958 reprint of Hearne's book, *A Journey from Prince of Wales's Fort in Hudson's Bay to the Northern Ocean* (MacMillan Company, Toronto, Ontario, 1958), the editor, Richard Glover, correctly recognized that "Samuel Hearne was, of course, another first class observer and reporter . . . head and shoulders superior to every other North American naturalist who preceded Audubon."

An observer, not a collector, Hearne was the first to give a recognizable description of the Ross's Goose, named *Anser rossii* by John Cassin some 80 years later:

FIG. 1. This portrait of Samuel Hearne, reproduced with permission from Stuart Houston (Houston, S., T. Ball, and M. Houston. 2003. Eighteenth-Century Naturalists of Hudson Bay. McGill-Queen's University Press, Montreal, Quebec), first appeared in *The European Magazine* in 1797 (original artist unknown).

> HORNED WAVEY. This delicate and diminutive species of the Goose is not much larger than the Mallard Duck. Its plumage is delicately white, except the quill-feathers, which are black. The bill is not more than an inch long, and at the base is studded round with little knobs about the size of peas, but more remarkably so in the males. Both the bill and feet are of the same colour with those of the Snow Goose. The species is very scarce at Churchill River, and I believe are never found at any of the Southern settlements; but about two or three hundred miles to the North West of Churchill, I have seen them in as large flocks as the Common Wavey, or Snow Goose. The flesh of this bird is exceedingly delicate, but they are so small, that when I was on my journey to the North I eat [ate] two of them one night for supper.

As the quotation above illustrates, many of Hearne's observations were practical in nature. Many species were numerous at that time. Similarly, Hearne noted that one Indian could kill twenty Spruce Grouse in a day with his bow and arrow and some would kill upwards of a hundred Snow Geese in a day, whereas the most expert of the English hunters would think it a good day's work to kill thirty. At Albany Fort in one season, sixty hogsheads (i.e., 220–245 liters each) of geese were salted away for winter consumption. Hearne also mentioned that Arctic Terns, which he ranked as being among "the elegant part of the feathered creation," occurred in flocks of hundreds; bushels of their eggs were taken on a tiny island.

Hearne once saw a flock of more than 400 Willow Ptarmigan near the Churchill River. The Indians had put framed nets on stakes and placed them over gravel bait to entice ptarmigan to gather under the net. The stake was then pulled to drop the net on top of the birds. Using this method, 3 people could catch up to 300 birds in 1 morning; in the winter of 1786, Mr. Prince at Churchill caught 204 with two separate pulls. Ptarmigan feathers made excellent beds; the feathers sold for three pence per pound. The smaller Rock Ptarmigan would not go under nets, but up to 120 could be shot in a few hours.

In Hearne's time, cranes, curlews, and Passenger Pigeons also were regularly shot for food; the latter flew in large flocks in the interior near Cumberland House where Hearne saw 12 killed at one shot. Whooping Cranes, only occasionally seen, most often occurred in pairs. He indicated that this largest crane was good eating, and its wing bones were so long and large that they were sometimes made into flutes. Hearne was the first to recognize two different species of curlew, the Hudsonian and the Eskimo. He also provided invaluable information concerning the northern edge of the Eskimo Curlew's breeding range—Egg River, on the west coast of Hudson Bay at 59° 30′ N, about 150 miles north of Churchill.

Hearne combined keen powers of observation with a deep appreciation for the natural world. His observations of the Ruffed Grouse, although precise and accurate, also convey a real sense of awe and wonder:

> THE RUFFED GROUSE. This is the most beautiful of all [grouse]. . . . They always make their nests on the ground, generally at the root of a tree, and lay to the number of twelve or fourteen eggs. . . . There is something very remarkable in those birds, and I believe peculiar to themselves, which is that of clapping their wings with such a force, that at half a mile distance it resembles thunder. I have frequently heard them make that noise near Cumberland House in the month of May, but it was always before Sun-rise, and a little after Sun-set.

Hearne did not, however, restrict his attention to edible birds; he also described small birds, such as the chickadee, or the ground nest of a White-crowned Sparrow at the root of a dwarf willow or a gooseberry. He understood the concept of bird migration, describing the Trumpeter Swan as the first species of waterfowl to return each spring, sometimes as early as late March, and frequenting the open waters of falls and rapids. He also named year-round residents, such as the Willow Ptarmigan and Arctic Hare. Hearne's understanding of sexual dimorphism showed in his remark that the male Willow Ptarmigan was larger than the female. His description of the body-size range among ptarmigans demonstrates his understanding of what was later to be described as Gaussian distribution.

Hearne noted that the pouch at the base of the pelican's beak had a capacity of three quarts and that, in the 1770s as well as today, muskrat houses were favorite nesting sites for Canada Geese. He evidently was the first to dissect the "windpipe" of an adult Trumpeter Swan, noting that the convoluted trachea passed into the broad and hollow breastbone of the swan and, after passing the length of the sternum, returned into the chest to join the lungs. He also dissected a Tundra Swan but failed to appreciate its lack of the extra perpendicular hump in the trachea that is present in the larger Trumpeter Swan.

While in England during the winter of 1782–1783, Hearne met Thomas Pennant and gave him a copy of his natural history sightings, a dozen years in advance of their posthumous publication. Pennant incorporated a number of Hearne's observations into *Arctic Zoology* (in 3 volumes, Robert Faulder, London, 1792). Five years after retiring to England in 1787, Hearne sold his manuscript, *A Journey from Prince of Wales's Fort in Hudson's Bay to the Northern Ocean,* to a publishing firm in London (A. Strahan and T. Cadell) for the unprecedented sum of £200. Only a month later, when only 47 years old, Hearne died "of the dropsy." His book, one of the greatest travel narratives ever written, appeared in print posthumously in 1795.

From my point of view, Hearne's account

of the large subspecies of Canada Goose (*Branta canadensis maxima*) best reveals his scientific bent. He met these very large geese on the Barren Grounds, but he did not call them Barren Geese because they summered there; rather, he named them after dissecting them and discovering an "exceeding smallness of their testicles." Hearne's observation of the unusually large race of geese with small testicles was confirmed more than a century and a half later in Harold C. Hanson's book, *The Giant Canada Goose* (Southern Illinois University Press, Carbondale, 1965). The book detailed how, in the 1960s, Giant Canada Geese were captured and banded as flightless young in Rochester, Minnesota, southern Manitoba, and southern Saskatchewan, after which they traveled north 1,600 km to molt (thus arriving later in the year than the breeding individuals). Because the geese were too young to breed, they had small testicles. This confirmed the phenomenon that Samuel Hearne, truly one of the most talented of the early North American naturalists, noted with such insight:

> BARREN GEESE. These are the largest of all the species of Geese that frequent Hudson's Bay, as they frequently weigh sixteen or seventeen pounds. They differ from the Common Grey Goose in nothing but size, and in the head and breast being tinged with a rusty brown. They never make their appearance in the Spring till the greatest part of the other species of Geese are flown Northward to breed, and many of them remain near Churchill River the whole summer. This large species are generally found to be male, and from the *exceeding smallness of their testicles,* they are, I suppose, incapable of propagating their species.

The original reference for this piece is S. Hearne, 1795, *A Journey from Prince of Wales's Fort in Hudson's Bay to the Northern Ocean,* A. Strahan and T. Cadell, London. The modern reference is S. Houston, T. Ball, and M. Houston, 2003, *Eighteenth-Century Naturalists of Hudson Bay,* McGill-Queen's University Press, Montreal, Quebec.—C. STUART HOUSTON; e-mail: houstons@duke.usask.ca

The Wilson Journal of Ornithology 118(4):580–585, 2006

Ornithological Literature

Compiled by Mary Gustafson

FIRE AND AVIAN ECOLOGY IN NORTH AMERICA. By Victoria A. Saab and Hugh D. W. Powell (Eds.). Studies in Avian Biology no. 30, Cooper Ornithological Society, Camarillo, California. 2005: vii + 193 pp., 20 tables, 12 maps, 8 other figs. ISBN: 0943610648. $18.00 (paper).—Formerly the purview of agency personnel and a handful of academics, over the last 30 years wildland fire management has entered the mainstream consciousness as a topic of debate and interest. This has been accompanied by a corresponding increase in attention paid by ornithologists to topics on fire ecology. This volume adds to the ever-growing list of fire-related papers and books, in this case providing a well edited and useful literature review specifically concerned with the effects of fire and fire exclusion on birds and their habitats.

This work is largely the result of a Partners In Flight symposium (held in 2002) that focused on patterns in human alteration of fire regimes and the consequences on bird populations and habitats. The introductory chapter provides an overall summary, highlights patterns, and suggests future research needs. While not a definitive treatment of all avian habitats found in North America, discussion of more than 40 North American ecosystems provides ample opportunity for the emergence of some broad patterns in fire regimes and avian responses. For example, habitats with naturally long fire-free periods have been less affected by fire exclusion practices because the period of fire exclusion is not markedly different from the normal fire-return interval.

Ten chapters summarize the current state of knowledge regarding fire and birds in the southwestern United States, California's oak woodlands, the maritime Pacific Northwest, sagebrush habitats, the Rocky Mountains, the boreal forests of Canada, central tallgrass prairies, eastern deciduous forests, grasslands and shrublands in New England, and southeastern pine savannas and native prairies. Many authors point out the lack of fire-effects data for particular habitats, and base projected fire effects on what is known about general avian habitat associations and responses to habitat change, or on the results of fire studies in similar habitats. For example, although fire is relatively common in California's oak woodlands, only one study has focused on the effects of an actual fire on birds in that system.

In total, the responses of more than 200 bird species to fire are discussed, with some predictable outcomes. For example, it is clear that frequent burning creates less favorable conditions for forest birds that nest low or on the ground, and that foliage gleaners prefer unburned habitats. The predictability of a given species' response, however, may not be straightforward: it may vary by region or with differences in fire size, intensity, frequency, and seasonal timing. In the case of Greater Sage-Grouse (*Centrocercus urophasianus*), an objective analysis suggests that prescribed fire—although often touted—may not have been overly successful as a management tool.

Although not part of the typical *Studies in Avian Biology* format, an index summarizing the effects of fire on different species would have been useful to workers concentrating on one or a few bird species. All 11 chapters are well-referenced, as evidenced by more than 900 sources listed in the Literature Cited section. Such a hefty Literature Cited section on the relatively narrow topic of fire and birds further increases this work's utility as a reference.

Several recurring themes appear in the chapters, including a call for additional research—especially experimental work on fire effects, which makes for good science and is entirely feasible in many prescribed fire scenarios. Response variables should focus on avian demographics, rather than on bird abundance, as is the case in many previous bird-fire studies. Well-stated was the premise that "understanding past fire regimes is of less practical value than investigating how present-day fires fit into the landscape and how they can be used to achieve management objectives." Given the clear need for more fire on the landscape, many of the authors suggest an approach to using prescribed fire that does not involve burning all the available acres in a short time period, but rather at a variety of temporal and spatial scales to produce a mosaic of different habitat and age classes. This well-reasoned approach to maintaining variation in the landscape might contrast with some practices, such as the large-scale application of frequent understory fires (as is typical in southwestern pine forests) in the Rocky Mountains, where a stand-replacing fire might be an objective.

Like most treatises on fire ecology, this one makes the obligatory call for less fire suppression with statements like "... it clearly seems reactive to continue battling naturally ignited fires burning within historic ranges of severity." Although understandable, such statements fail to appreciate the current impracticality of letting most wildfires burn, considering that modern wildlands comprise a complex mix of fire-adapted vegetation, small remnant patches of vulnerable special habitats (e.g., riparian and stands of old-growth forest), areas of increased flammability due to the presence of exotic plants and other buildups of fuels, and at-risk investments (e.g., conifer plantations and other anthropogenic improvements). Such a landscape, combined with dynamic weather patterns, a political atmosphere driven by special interest groups (e.g., proponents of scenic values for tourism), public health (e.g., smoke management) and safety concerns, and an increasingly litigious society make risk-averse decision makers unlikely to push too hard for expanded let-burn policies any time soon. While many authors call for expanded prescribed burning programs, large-scale application of fire as the primary fuels treatment could only be done with massive (and seemingly unlikely) increases in prescribed fire budgets. Thus, although fire is an appealing treatment for ecosystem restoration and management, it seems likely that mechanical thinning, livestock grazing, and other treatments intended as surrogates for fire will provide land managers with solutions over the short run, so researchers should probably look a bit harder at such options. However, since much of the discussion in this volume deals with responses of birds to habitat change, not necessarily their responses to fire, *per se,* the information provided will facilitate planning for, and implementation of, a range of habitat treatments.

In light of the ongoing public debate regarding forest health and fire, especially welcome was a statement contrasting the effects of fuels treatments involving commercial harvest of large trees with those treatments intended to remove highly combustible, small-diameter fuels. We can only hope that forest managers also heed the cautions provided by many authors on post-fire salvage logging, which can easily reverse any benefits the burn may have provided to certain groups of birds, especially cavity-nesters.

Fire and Avian Ecology in North America will be an interesting and useful addition to the reference libraries of agency biologists, fire managers, ecologists, and others involved in fire and fuels issues. I recommend this book.—JOHN E. HUNTER, U.S. Fish and Wildlife Service, Arcata, California; e-mail: John_E_Hunter@fws.gov

BIRDS OF WESTERN AFRICA. By Nik Borrow and Ron Demey. Princeton University Press, Princeton, New Jersey. 2004: 512 pp., 147 color plates, 3,000+ color illustrations. ISBN: 0691123217. $40.00 (paper).—*Birds of Western Africa,* by N. Borrow and R. Demey, was originally published in 2001 by Christopher Helm, London (hard cover), whereas this volume was released as part of the Princeton Field Guide series (soft cover). This magnificent field guide covers all 1,285 species of birds found within the present region of Western Africa, which the authors define as extending from Senegal and southern Mauritania east to Chad and the Central Africa Republic, and south to Congo, including Cape Verde and the Gulf of Guinea islands. A color-shaded map shows the location of each country.

The introduction provides information on changes to scientific and common names, including standardizations of English names, made since the 2001 publication. Name changes are those recommended by David and Gosselin (David, N. and M. Gosselin. 2002. Gender agreement of avian species names. Bulletin of the British Ornithology Club 122: 257–282) (David, N. and M. Gosselin. 2002.

The grammatical gender of avian genera. Bulletin of the British Ornithology Club 122:14–49). The introduction is followed by an excellent review of the climate, topography, habitats, and restricted ranges of certain species; a glossary of terms; and excellent illustrations and descriptions for morphological terminology. Western Africa has no fewer than 87 restricted-range species occurring in 7 areas of avian endemism, including the Cape Verde Islands, Annobón, Sáo Tomé, Principe, Upper Guinea forests, Cameroon and Gabon lowlands, and Cameroon mountains. Another four species are considered confined to restricted-range areas in the Upper Niger valley, southwest Nigeria, the Lower Niger valley, and the Gabon–Cabinda coastal area. For the regions noted above, the authors list the species that are highly threatened.

For each species, the authors provide a color distribution map and authoritative descriptions of distinctive characteristics needed to identify the species. For nearly all species, they also provide color illustrations of the species. All the illustrations in this compact field guide were rendered by the same acclaimed bird artist, Nik Borrow, and their layout is similar to that of the Peterson Field Guides; however, they lack Peterson's arrows pointing out distinctive species characteristics that would have made it easier to identify species in the field. A unique feature of this book is the set of black and white plates illustrating nest construction for 20 species of weaver birds.

This is the first field guide to cover Western Africa exclusively, and it should enable birders to identify any species found within the 23 countries and territories covered within the text. The book is a concise, authoritative, and reasonably priced guide available from a leading university publisher that employs a critical review system. We highly recommend this must-have reference for anyone interested in the birds of Western Africa or concerned with ornithology on a worldwide basis, and/or for those who wish to augment their field guide collection. The cover design is attractive, and should catch the eye of bird lovers. The publishers should be commended for producing another excellent, reasonably priced monograph.—HARLAN D. WALLEY and PATRICIA A. RUBACK, Department of Biology, Northern Illinois University, DeKalb, Illinois; e-mail: hdw@niu.edu and pattyruback@hotmail.com

RAPTORS AND OWLS OF GEORGIA. By Rafael A. Galvez, Lexo Gavashelishvili, and Zura Javakhishvili. Georgian Centre for the Conservation of Wildlife and Buneba Print Publishing, Tibilsi, Georgia. Distributed by NHBS, United Kingdom. 2005: 128 pp., 47 color maps, 447 color illustrations. ISBN: 999407718X. £14.99 (paper). [In English and Georgian]—This is the first field guide to cover all the raptors and owls recorded in Georgia, and a first for the Caucasus region. It describes the 45 raptor species recorded in the country, including the breeding species, seasonal residents, migrants, and rare visitors. The status of each species is color-coded on an accompanying distribution map of Georgia.

The field guide has a foreword by the authors and an introductory chapter comprising several sections, the first of which is a short explanation of raptor classification. This is unusual in that it includes silhouettes of the major families of raptors and owls and explains how to distinguish them in the field. The section on "wing attitudes" is especially interesting because it shows the novice what to expect in the field under different weather conditions. The next section presents a short description of raptor migration and Georgia's role in the Palearctic flyways. There is also a section on the conservation status of nocturnal and diurnal raptors from a continental perspective, with a brief history of Georgia and a map showing the locations of Georgia's 27 protected areas. The section on how to use the book should be read carefully to gain a better understanding of the maps and accompanying symbols used in the species accounts.

Following the introductory chapter are the 45 species accounts. Each species is allocated a minimum of two facing pages. Provided on the left (text) page of each account is the species' common name (alternative additional names are listed parenthetically) and Latin names (including subspecies inhabiting Georgia), biometric data (body length, wingspan, and body mass), and the known or extrapolated number of breeding pairs in the country.

The text also briefly describes the species' diagnostic identification features. Here the authors have been very innovative: they have emphasized the most prominent features by underlining them and pointing to them in the species' illustration on the facing page; a short comparison with potentially confusing species is also provided. Additional text provides an aid to a better understanding of the behaviors and habitats occupied by the species. Other natural history information provided includes the species' foods, nest characteristics, clutch size, egg size and laying period, and the number of days in the incubation and nestling periods; also mentioned is how many years it takes an individual to reach sexual maturity. Lastly, the authors discuss the species' conservation status and population trend in Georgia. A color-coded map shows the species' year-round distribution.

The facing (illustration) page depicts the species. I found it very instructive that the authors chose to show each of the sexes in separate columns and, where relevant, they illustrated different morphs at different ages. Lines point to the most diagnostic features to look for during field observation. I especially enjoyed the sketches that show habitats in which the species should be found, or engaged in some unique behavior, and the fact that—interspersed between the species accounts—there are two pages of field drawings of species addressed in the previous pages. These drawings illustrate habitats, behaviors, prey, inter- and intra-specific interactions, and nest structures and locations.

I greatly appreciate this compact field guide. It will be a good companion for raptor watchers who will find that it is relevant not only to Georgia but also to most of the neighboring countries (i.e., all of the Caucasus region). The only flaws I found in the book were in the illustrations. A few of the drawings contain errors, including some that do not correctly depict the raptor's exact "jizz" and posture; examples of this problem may be found on page 83 in the drawings of Honey Buzzards. I also found the plates too dark. I have handled hundreds of raptors every year for more than a decade and know these birds up close—the colors of most are not as dark as they are in the illustrations. This criticism, however, should not put off raptorphiles or birdwatchers that need a good raptor identification guide for that part of the world. Furthermore, proceeds from the sales of this book are donated to the Georgian Centre for the Conservation of Wildlife and to conservation efforts within the region. On the whole, this is a worthwhile undertaking by local ornithologists whose worthy endeavors within the region deserve recognition.—REUVEN YOSEF, International Birding and Research Center, Eilat, Israel; e-mail: ryosef@eilatcity.co.il

BIRDS OF MEXICO AND CENTRAL AMERICA. By Ber Van Perlo. Princeton University Press, Princeton, New Jersey. 2006: 336 pp., 98 color plates. ISBN: 0691120706. $29.95 (paper).—The format of this newest guide in the Princeton Illustrated Checklist series is best described as an abbreviated field guide format. The guide covers Mexico and all of Central America to Panama—a vast area containing a huge number of species (1,574) to illustrate in a single guide. The 98 color plates have thumbnail illustrations of the birds and a brief text (on the facing, or a nearby, page). Maps showing geographic distributions follow the color plates. Other than an index, table of contents, and brief introductory pages, that is the total extent of this guide. This book should not be viewed as a replacement for books like Howell and Webb's excellent, comprehensive guide (Howell, S. N. G. and S. Webb. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press, New York), which provides a much more complete account for each species, including in-depth coverage of identification, distribution, taxonomy, vocalizations, and more. This is a compact and useful guide to tote in the field, however it only complements rather than replaces handbooks like Howell and Webb's guide.

The plates are generally well done and illustrate all species found in the area, including hypothetical or rare species, whereas the Howell and Webb guide omits illustrations of many North American migratory passerines and provides only black and white drawings for some waterbirds. The plates in Princeton's Illustrated Checklist, however, do not depict all the plumages essential for identification;

for example, immature plumages of Great Blue Heron (*Ardea herodias*), Cooper's Hawk (*Accipiter cooperii*), Cedar Waxwing (*Bombycilla cedrorum*), Loggerhead (*Lanius ludovicianus*) and Northern (*L. excubitor*) shrikes, Scissor-tailed Flycatcher (*Tyrannus forficatus*), Prairie Warbler (*Dendroica discolor*), and Chestnut-sided Warbler (*Dendroica pensylvanica*) are not included. The plates and text will not help with more difficult identifications; even adult Glossy (*Plegadis falcinellus*) and White-faced (*P. chihi*) ibis, or Rusty (*Euphagus carolinus*) and Brewer's (*E. cyanocephalus*) blackbirds will be unidentifiable if only this guide is used. The immature White-tailed Hawk (*Buteo albicaudatus*) is labeled in the text as not identifiable, and the illustration does not show one representative age, making correct identification impossible.

Unlike many Latin American guides that include North American migrants, the plates of these species are fairly well done. I could quibble with illustrations like that of the Pine Siskin (*Carduelis pinus*), but in general the illustrations are accurate. Indications of changes in scale within a given plate were not provided; for example, plate 77 depicts Green Shrike-Vireo (*Vireolanius pulchellus*) and gnatcatchers as being the same size. On another plate, the Red-winged Blackbird (*Agelaius phoeniceus*) male and female are the same size and are illustrated as larger than the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). Among the illustrations of neotropical species, some could have been better portrayed or benefitted from another view. For example, the unique tail pattern of the Olivaceous Piculet (*Picumnus olivaceus*) is not illustrated or described, and the tuft on the Tufted Flycatcher (*Mitrephanes phaeocercus*) is very weak and the illustration does not look much like the species. The text accompanying the illustrations is concise and provides codes for range, status (endemic, hypothetical, rare, etc.), and seasonality. There are several problems, however, including a reversed caption or plate number (Baltimore [*Icterus galbula*] and Orchard [*I. spurious*] orioles), and inappropriate abbreviations of common names (e.g., "Grosbeak" for Blue Grosbeak, *Passerina caerulea*). Most common names and taxonomy follow the American Ornithologists' Union, but there are exceptions, including the use of the common name Gray Plover for Black-bellied Plover (*Pluvials squatarola*) and the split of Stephen's (Mexican) Whip-poor-will (*Caprimulgus arizonae*) from Whip-poor-will (*Caprimulgus vociferus*).

The text for each plate often extends to the next page, adjacent to the following plate, the text for which then also runs over to the next page, and so on until half the text on any one page may pertain to the current plate and half to the preceding plate. Eventually it evens out (or additional textual pages are included), but this makes the guide more difficult to use (albeit slightly). The maps are understandably small, as there are 27 maps per page, each including the species' name, plate number, and the species' number on the plate to aid cross-referencing between the maps and plates. A neat innovation is that the maps show the species' detectabilities (common to frequent, frequent to uncommon, uncommon to rare; or a percent likelihood of detectability) and status (resident, transient, present in northern winter or northern summer). This allows the maps to convey more information than just presence/absence for a given location, making them extremely useful. Locations of rarities or isolated populations are identified with cross hairs or stars.

I have quibbled over some issues in this guide, but I am very pleased to have it available and I will give it the greatest complement I can give to a field guide; I will use it. I will carry this guide in the field and leave both *A Guide to the Birds of Mexico and Northern Central America* and *The Sibley Guide to Birds* (Sibley, D. A. 2000. The Sibley Guide to Birds. Alfred A. Knopf, New York.) in the car. This guide will be especially useful for those unfamiliar with the North American migrants and who want illustrations of the migrant and resident birds in one small volume. If this guide were to be translated into Spanish, it would become the standard guide for use in Mexico and Latin America; thus, publication of a Spanish version should be a high priority to benefit conservation and education in the region.—MARY GUSTAFSON, Rio Grande Joint Venture, Texas Parks and Wildlife Department, Mission, Texas; e-mail: mary.gustafson@tpwd.state.tx.us

FALCONRY IN LITERATURE. By David Horobin. Hancock House, Surry, British Columbia, Canada. 2004: 240 pp., 1 color drawing, numerous line drawings and sketches from older books, 21 black & white photographs. ISBN: 0888395477. $50.00 (cloth).—I am not a practicing falconer, nor do I have much experience in falconry as a hobby, a sport, or a trade. I have always had an interest in falconry, however, because I have been aware of its historical role and was exposed to it by some of the most respected conservationists in the field.

Falconry today is a controversial subject. This is especially so because we are aware of the dangers that wild populations face, and their related conservation status is endangered by those who have the financial resources to acquire raptors. The high prices that certain raptors bring in falconry circles, and the trade in eggs, young, and birds taken from the wild, are raising a lot of questions about the validity of continuing the practice of falconry. Few are the countries where falconry is regulated by legislative authorities that understand the subject.

Having said this, I was fascinated by this book. It brings to the reader writings by European poets and dramatists of the Medieval and Renaissance periods. The book opens a window to how falconry was perceived in the past and the infatuation of the aristocratic classes with birds of prey. This book is a classical English literature review of texts ranging "from Chaucer to Marvell" and explores the meaning (and confusion, for that matter) of falconry. This is a book for the intellect that is able to see beyond the sport of flying one's raptor and provides a perspective on the history in which the sport is steeped. The author's knowledge of birds and their natural history is presented in a very scholarly manner. I strongly recommend this book for those practicing falconers who like a good evening read in the armchair—for me it certainly was a pleasant change from the current television programming.—REUVEN YOSEF, International Birding & Research Center, Eilat, Israel; e-mail: ryosef@eilatcity.co.il

The Wilson Journal of Ornithology 118(4):586–592, 2006

PROCEEDINGS OF THE EIGHTY-SEVENTH ANNUAL MEETING

SARA R. MORRIS, SECRETARY

The eighty-seventh annual meeting of the Wilson Ornithological Society (WOS) was held Tuesday, 3 October, through Saturday, 7 October 2006, at the World Trade Center in Veracruz, Mexico, in joint session with the American Ornithologists' Union; Association of Field Ornithologists; Sección Mexicana de Consejo Internacional para la Preservación de las Aves, A. C.; Cooper Ornithological Society; Raptor Research Foundation; Society of Canadian Ornithologists/Société des Ornithologistes du Canada; and Waterbird Society. This joint meeting, the fourth quadrennial meeting of professional North American ornithological societies, was called the IV North American Ornithological Conference (NAOC). The conference was themed, "Wings Without Borders/Alas Sin Fronteras." The steering committee was co-chaired by Charles M. Frances and José L. Alcántara and included Bonnie S. Bowen, Eduardo E. Iñigo-Elias, M. Ross Lein, Cecilia Riley, Betty Ann Schreiber, and Doris Watt. Juan E. Martínez Gomez and Ernesto Ruelas Inzunza co-chaired the local committee. The Conference Administration/Finance Committee co-chairs were Bonnie S. Bowen, Frank B. Gill, and Helen Schneider Lemay; the Fundraising Committee co-chairs were Frank B. Gill and Eduardo E. Iñigo-Elias. The meeting was co-hosted by the Instituto de Ecología, A.C.; Veracruz Visitors and Conventions Bureau; Consejo Regulador del Café Veracruz, A.C.; Universidad Veracruzana; Island Endemics Foundation/Endemicos Insulares, A.C.; Municipality of Boca del Río; and Consejo de Promoción Turística de México.

The Council met from 13:33 to 17:43 CDT in the Centro de Negocios-2 room of the Hotel Galería Plaza on Monday, 2 October. On Tuesday, 3 October, Hotel Mocambo hosted an opening reception from 18:00 to 22:00 on the terraces and around the pool. Each of the next four mornings began with a plenary and presentation of different society awards in the World Trade Center Ulúa Rooms 1–3. Scientific papers were presented during eight concurrent sessions held in the late mornings and afternoons in the World Trade Center Ulúa and Olmeca Rooms. Business meetings of the individual societies were conducted in the early evenings beginning at 17:35. Poster sessions were held from 19:30 to 22:00 on Wednesday, 4 October, and Friday, 6 October.

The scientific program committee was co-chaired by John R. Faaborg, Juan Francisco Ornelas, and María del Coro Arizmendi. The U.S. members of the scientific program committee were Al Dufty, Elizabeth A. Schreiber, George Wallace, Beth Wallace, Peter Lowther, and Steven C. Latta; Mexican members of the committee were Octavio Rojas, Carlos Lara, Flor Rodríguez, Adolfo G. Navarro S., Alejandro Espinosa de los Monteros, and J. Fernando Villaseñor G. The scientific program consisted of a total of 1,239 presentations, including 4 plenary talks, 336 oral papers contributed to 24 symposia, 368 oral papers in 38 general sessions, and 531 poster presentations split between two poster sessions, each of which was divided into 46 different topics. Additionally, there were 17 workshops organized in conjunction with the conference. On Thursday, 5 October, Jed Burtt introduced the Margaret Morse Nice lecture, which was the conference plenary on that day. Jed presented the biography of Margaret Morse Nice in Spanish and introduced the speaker, Gary Stiles, in English. After the lecture, President Doris Watt presented Gary Stiles with the Margaret Morse Nice medal.

The Student Affairs Committee—co-chaired by Andrea Cruz-Angón and James W. Rivers and including Eben Paxton, Doug Robinson, Julie Garvin, José Luis Rangel-Salazar, Vicki Garcia, Lori Blanc, Jackie Nooker, and Jean-Michel DeVink—organized a number of activities for students. A Grant Proposal Workshop was held on Tuesday, 3 October. The professional societies, including WOS, contributed financial support for a student-professional ornithologist social on Thursday evening. The social was followed by a Jeopardy-style quiz bowl for nine teams of three students each, which was played energetically and boisterously, to the entertainment of all assembled. Students also were given the opportunity to be matched with professional ornithologists in a student mentoring program that provided one-on-one interaction between students and researchers in their areas of interest.

A variety of field trips before, during, and after the conference delighted participants with opportunities to see Mexican resident and Neotropical migratory birds. Daily trips during the conference took participants to the State Park Arroyo Moreno to see the mangroves and to Cardel and Chichicaxtle to see migrating raptors. Four-day, pre- and post-conference tours included birding, cultural, and archaeological sites; birds and butterflies of lowlands and highlands in Central Veracruz; Catemaco rainforest; Veracruz coffee plantations and highlands; and Veracruz highlands. One-day trips before the conference were made to coastal habitats and lowland tropical forest at La Mancha and Quiahuiztlan, mangroves and wetlands of Alvarado and Tlacotalpan, and transition zones between lowland and cloud forests at El Mirador and Las Cañadas. After the conference, day trips included visits to conifer forest and cloud forest of Las Minas and Los Humeros, tropical rain forest of Los Tuxtlas, and cloud forest and Isthmus plateau in Oaxaca, the state bordering Veracruz.

The conference was closed by a Fiesta Jarocha—with a social hour, a seated dinner, entertainment by the Universidad Veracruzana, including Ballet Folklórico and music, and the announcement of students receiving student presentation awards and honorable mentions. Although the final announcements were completed at 21:35, the music and dancing continued into the night.

BUSINESS MEETING

President Doris Watt called the business meeting to order at 17:59 on 4 October in the Olmeca-5 Room of the World Trade Center. She recognized a quorum and thanked those assembled for attending.

Secretary Morris presented a summary of the Council meetings, which were held Saturday, 18 March, at Hawk Mountain in Pennsylvania and Monday, 2 October, in Veracruz. As of September 2006, the Wilson membership stood at 1,937, which includes 268 students and 166 new members. We also have 417 institutional subscriptions to the *Wilson Journal of Ornithology,* which is down from 463 last year. As part of the Ornithological Societies of North America (OSNA) report, Council learned of several WOS members who passed away during the last year, and Secretary Morris asked those assembled to stand while she read the following names: Stanley H. Anderson (Laramie, WY), Carl N. Becker (St. Petersburg, FL), Herbert L. Cilley (Center Strafford, NH), James F. Clements (Temecula, CA), Abbot S. Gaunt (Columbus, OH), A. Durand Jones (Estes Park, CO), Frank J. Ligas (Naples, FL), Karl H. Maslowski (Cincinnati, OH), Richard T. Paul (Tampa, FL), Mario A. Ramos (Washington, DC), Clayton G. Rudd (Moose, WY), Haven H. Spencer (Dover, MA), Mardi Stoffel (Rochester Hills, MI), and Jeff Swinebroad (Montgomery Village, MD).

After members were seated, Secretary Morris commented that the Schneider Group continues to manage the membership and executive director duties for OSNA. Membership renewal was much smoother this year and the renewal notices for next year were mailed recently, but please let one of the Council officers know if you are experiencing difficulty with your membership. Council thanked the Investing Trustees for their excellent work in managing the investments, and directed them to continue managing the WOS portfolio for total return.

The Council approved offering a free membership to students who are not currently members of the Society and who attend and present a paper or poster at a WOS annual meeting (one that is not held in conjunction with the American Ornithologist Union and Cooper Ornithological Society). Council also increased the funds allotted for student travel from $5,000 to $10,000 for the North American Ornithological Conference (NAOC), which funded 25 students at $400 each. Additionally, Council approved a one-time contribution of $7,500 to the Ornithological Council for revisions to the *Guidelines for the Use of Wild Birds in Research.*

The Council elected Clait Braun as editor of *The Wilson Journal of Ornithology* for Volume 119. Council expressed sincere gratitude for Jim Sedgwick's work in getting the *Wilson Bulletin* back on its publication schedule and steering changes that resulted in the new *Wilson Journal of Ornithology,* an updated and revitalized journal. Council accepted a recommendation to appoint associate editors for the journal. Council also approved archiving *The Wilson Bulletin* and its successor *The Wilson Journal of Ornithology,* in JSTOR (Journal Storage, The Scholarly Journal Archive) and approved a licensing agreement with EBSCO Information Services to include *The Wilson Bulletin* and its successor, *The Wilson Journal of Ornithology,* in their database. There is a three-year lag between publication and availability on JSTOR and EBSCO. President Watt has established a new *ad hoc* Web site Committee, chaired by Bob Curry, to spearhead an updated Web presence for the Society.

At the 2007 annual meeting, the Society will present the first Klamm Awards: the William and Nancy Klamm Service Award and the Klamm Outstanding Undergraduate Student Paper Awards (one for the best oral paper and a second for the best poster).

The Council approved the following future meetings: 2007 in the Boston, Massachusetts, area, hosted by Massachusetts Audubon; 2008 in southern Mississippi, hosted by Frank Moore; and 2009 in Pittsburgh, Pennsylvania, co-hosted by the National Aviary and Powdermill Avian Research Center of the Carnegie Museum of Natural History. Council also approved involvement in the planning of the next NAOC and Dale Kennedy will be the WOS representative on the planning committee.

Treasurer, Melinda Clark, presented her Treasurer's Report and Doris Watt presented highlights of the 2005 Editor's Report from Jim Sedgwick and an update from Clait Braun on the establishment of the new editorial office.

Doris Watt presented the report of the Nominating Committee, chaired by Robert C. Beason and including Mary Bomberger Brown, Sara R. Morris, and Timothy J. O'Connell. The committee recommended the following slate of candidates: President, Doris J. Watt; First Vice-President, James D. Rising; Second Vice-President, E. Dale Kennedy; Secretary, John Smallwood and W. Herbert Wilson; Treasurer, Melinda M. Clark; and Members of Council (2006–2009), Carla J. Dove, Greg H. Farley, and Mia R. Revels. President Watt thanked the nominating committee and asked for any nominations from the floor. Hearing none, she closed nominations following a motion by Jerry Jackson, seconded by Peter Stettenheim. Judy McIntyre moved that the Secretary cast a single ballot for the slate of unopposed candidates; Bob Curry seconded that motion, which passed unanimously. Secretary Morris cast the ballot, electing those officers and council members. John Smallwood was elected Secretary by paper ballots of the membership.

The Society's awards (see below) were announced during the business meeting (except for the student presentation awards, which were announced at the banquet). President Doris Watt announced the Edwards Prize recipients for 2004 and 2005. Secretary Sara

Morris announced the recipients of the research awards. Bob Curry presented a commendation, which was approved by the membership by acclamation following a motion by Chan Robbins, seconded by Mary Bomberger Brown.

President Watt adjourned the meeting at 18:30 after a motion from Tim O'Connell, which Jerry Jackson seconded.

MARGARET MORSE NICE MEDAL

(for the 2006 WOS plenary lecture)

Dr. F. Gary Stiles, "Ornithology in a troubled country: progress, problems, and recent work on nectar-feeding birds."

EDWARDS PRIZE

(for the best major article in volume 116 of *The Wilson Bulletin*)

Carolyn B. Meyer, Sherri L. Miller, and C. John Ralph, "Stand-scale habitat associations across a large geographic region of an old-growth specialist, the Marbled Murrelet." Wilson Bulletin 116: 197–210.

EDWARDS PRIZE

(for the best major article in volume 117 of *The Wilson Bulletin*)

J. Daniel Lambert, Kent P. McFarland, Christopher C. Rimmer, Steven D. Faccio, and Jonathan L. Atwood, "A practical model of Bicknell's Thrush distribution in the Northeastern United States." Wilson Bulletin 117:1–11.

LOUIS AGASSIZ FUERTES AWARD

Chris Merkord, University of Missouri–Columbia, "Altitudinal migration in the Andes of southeastern Peru."

PAUL A. STEWART AWARDS

Kathleen Coates, Purdue University, "Swamp Sparrow (*Melospiza georgiana*) population dynamics and breeding bird communities at restored and natural marshes."

Kristen M. Covino, University of Maine–Orono, "The influence of an ecological barrier on directional decisions of nocturnal migrants."

Ana Maria Gabela, University of Massachusetts–Amherst, "Site fidelity and human impact on the Medium Ground Finch (*Geospiza fortis*) on Santa Cruz, Galapagos Islands."

Harry R. Jageman, University of Idaho, "Habitat use and ecology of Northern Pygmy Owls (*Glaucidium gnoma*)."

Alex Jahn, University of Florida, "Testing proximate hypotheses of bird migration in a forgotten migratory system."

Jason Townsend, SUNY College of Environmental Science and Forestry, State University of New York, "The role of sexual segregation in the winter ecology of the Bicknell's Thrush."

GEORGE A. HALL/ HAROLD F. MAYFIELD AWARD

(formerly the Margaret Morse Nice Award)

Karla Kinstler, "Vocal repertoire of the Great Horned Owl."

Selection committee for the Nice Medal—Charles Blem (Chair), Dale Kennedy, James Rising, and Doris Watt; for the Edwards Prize—James A. Sedgwick (Chair); for the Fuertes and Stewart Awards—James D. Rising (Chair), Clait Braun, Richard Conner, Dale Kennedy, Alex Mills, David Podlesak, Craig Rudolph, and Doug White; and for the Wilson and Lynds Jones Prizes—Kevin Omland and Katherine Renton (co-chairs of the NAOC Student Presentation Awards Committee that awarded 15 unranked best student papers at the conference). The recipients of the WOS travel Awards were chosen by the NAOC Student Awards Committee, composed of Matthias Leu, Mike Webster, Patricia Escalante, Kim Sullivan, and Tom Sherry.

ALEXANDER WILSON PRIZE

(for a student oral paper, one of 15 unranked best student papers presented at the NAOC)

Corey E. Tarwater, University of Illinois at Urbana–Champaign, "Life history implications of the post-fledging period in a Neotropical passerine./ Implicaciones del período posterior al emplumamiento para la historia de vida de un ave paserina Neotropical."

LYNDS JONES PRIZE

(for a student poster, one of 15 unranked best student posters presented at the NAOC)

Chris J. Clark, University of California–Berkeley, "Are hummingbird dive-noises vocal or non-vocal?/Los ruidos del vuelo en picada de los colibríes ¿son vocales o no vocales?"

COMMENDATION

WHEREAS, the WOS held its 2006 annual meeting in Veracruz, Mexico, as part of the fourth NAOC; and

RECOGNIZING that the conference represents one of the most significant ornithological gatherings in history, offering members of the WOS opportunities to socialize and share scientific information about birds with ornithologists from throughout North America and beyond; and

RECOGNIZING that this unprecedented event has been made possible only by the dedicated efforts of a large, international group of ornithologists and friends;

THEREFORE BE IT RESOLVED that the WOS thanks Juan E. Martínez Gomez and Ernesto Ruelas Inzunza, the rest of the local committee, the NAOC Steering Committee and other committees, and the Veracruz community for making the conference an extraordinarily valuable and enjoyable event.

REPORT OF THE TREASURER

OPERATING BUDGET FOR FISCAL YEAR 2006 AND 2007

2006 Budget Amended and Approved at Council Meeting, 18 March 2006
2007 Budget Amended and Approved at Council Meeting, 2 October 2006

	2007 Proposed Budget	2006 Annual Budget	2005 Actual Budget	2005 Annual Budget
Revenue				
Contributions	$ 1,200	$ 1,000	$ 1,289	$ —
Student Travel Research Fund	—	—	126	
Van Tyne Library Book Fund	—			
Sales—Back Issues	518	—	563	
Sales—Books (Van Tyne Library)	500	900	921	
Subscriptions	17,317	18,000	18,769	10,000
Page Charges	15,506	16,750	16,615	8,000
Royalties	3,409	1,600	1,688	1,000
BioOne Electronic Licensing	10,760	10,055	10,055	10,055
Mailing List Rental Income	660	500	652	
Memberships	31,332	40,000	37,499	46,000
Other Income	—	2,000	—	4,000
Total Revenue from Operations	**$ 81,202**	**$ 90,805**	**$ 88,176**	**$ 79,055**
Expenses				
Journal Publication Expenses				
Editorial Honorarium	$ 4,000	$ —	$ —	$ —
Editor Travel/Supplies	1,000	230	226	—
Editorial Assistance	25,000	55,000	53,373	55,000
Copyright Expense	48	50	48	—
Printing—Journal	64,400	65,000	64,336	60,000
Printing Color Plates	2,400	2,500	2,472	—
Total Journal Expenses	**$ 96,848**	**$ 122,780**	**$ 120,455**	**$ 115,000**
Operating Expenses				
Postage and Mailing—Back Issues	$ 440	$ 320	$ 312	$ —
Storage—Back Issues	680	1,400	1,379	2,000
Van Tyne Library Expenses	1,500	1,500	1,451	4,000
OSNA Management Services	21,000	21,000	20,428	25,000
Credit Card Fees	1,100	1,200	1,138	—
Travel Expenses—OSNA Representative	1,500	1,800	1,758	—
Travel Expenses—General	450	5,000	2,465	5,000
Travel Expenses—Ornithological Council	200	900	873	—
Meeting Expenses	1,000	1,500	10,170	15,152
Accounting Fees	4,500	4,500	3,627	5,580
Insurance—D&O	1,425	1,500	1,401	1,200
Office Supplies	570	300	292	1,000
Postage—General	260	260	254	—
Other Expenses	—	250	250	—
Filing Fees	5	5	5	—
Discretionary Expenses	3,000	3,500	—	4,000
Total Operating Expenses	**$ 37,630**	**$ 44,935**	**$ 45,802**	**$ 62,932**
Awards				
Hall/Mayfield	$ 1,000	$ 1,000	$ —	$ 1,000
Stewart	3,000	3,000	2,000	2,000
Fuertes	2,500	2,500	2,500	2,500
Wilson, Lynds Jones, Klamm	1,200	1,200	500	500
Student Travel Grants	5,000	10,000	2,600	5,000
Nice Award Expenses	3,000	6,800	2,893	5,800
Total Awards Expenses	**$ 8,000**	**$ 24,500**	**$ 10,493**	**$ 16,800**

Contributions				
Support—Ornithological Council	$ 9,000	$ 9,000	$ 9,000	$ 9,000
Support—Ornithological Council (restricted to revision costs)	7,500	—	—	—
American Bird Conservancy Dues	250	250	—	250
American Association for Zoological Nomenclature Dues	250	250	—	250
Total Contributions	**$ 17,000**	**$ 9,500**	**$ 9,000**	**$ 9,500**
Total Expenses	**$ 159,478**	**$ 201,715**	**$ 185,750**	**$ 203,982**
Expenses in Excess of Revenue Before Investment Income	**$ (78,276)**	**$ (110,910)**	**$ (97,574)**	**$ (124,927)**
Investment Activity				
Revenue				
Investment earnings (budgeted)	$ —	$ 70,000	$ —	$ 126,718
Realized gain/loss—Merrill Lynch	23,612		62,904	
Realized gain/loss—Howland	18,968		47,045	
Realized gain/loss—Sutton	5,812		13,034	
Unrealized gain/loss—Merrill Lynch	36,722		(51,548)	
Unrealized gain/loss—Howland	29,887		(69,590)	
Unrealized gain/loss—Sutton	4,794		(9,339)	
Investment earnings—Merrill Lynch	20,000		25,564	
Investment earnings—Howland	25,000		46,575	
Investment earnings—Sutton	4,200		3,731	
Total Revenue from Investment Activity	**$ 168,995**	**$ 70,000**	**$ 68,376**	**$ 126,718**
Investment Fees	25,091	22,000	21,660	—
Investment Revenue in Excess of Expenses	**$ 143,904**	**$ 48,000**	**$ 46,716**	**$ 126,718**
Total Revenue in Excess of Expenses	**$ 65,628**	**$ (62,910)**	**$ (50,858)**	**$ 1,791**
Investment Principal Needed to Cover Deficits		**62,910**		

STATEMENT OF FINANCIAL POSITION

31 December 2005

Assets		
Cash Investments		
Merrill Lynch—Cash	$ (2,427)	
Coamerica—Van Tyne Checking	1,354	
Van Tyne University Michigan Account	353	
Sutton Fund—Cash Equivalents	7,557	
Howland Management—Cash Equivalent	118,397	
Total Cash and Cash Equivalents		$ 125,233
Other Investments		
Merrill Lynch—Common Stocks	$ 689,356	
Merrill Lynch—Corporate Bonds	63,461	
Merrill Lynch—Mutual Funds	26,982	
Sutton Fund—Equities	125,415	
Sutton Fund—Corporate Bonds	10,033	
Howland Management—Equities	1,131,130	
Howland Management—Fixed Income	301,914	
Total Other Investments		**$ 2,348,291**
Total Assets		$ 2,473,524

Fund Balances		
Restricted Funds—Sutton Fund	$ 143,005	
Unrestricted Funds	829,937	
Net Income	(50,858)	
	779,079	
Fund Balance—Klamm	1,551,441	
Total Fund Balances		**$ 2,473,524**

Melinda Clark, *Treasurer*

EDITOR'S REPORT—2005

The Wilson Bulletin Editorial Office received a total of 162 manuscripts during 2005 (compared with 135 in 2004 and 130 in 2003). All papers received three peer reviews, except in rare instances when a referee failed to complete and return a review (<5% of cases). Correspondence from authors and referees was handled promptly (usually within 3 days of receipt). I accepted 18% and rejected 24% of manuscripts received in 2005, and returned the remainder (58%) to authors for extensive revision or revision and re-review. Volume 117 consisted of 41 major papers and 20 short communications, totaling 403 pages (456 total journal pages); each issue had a color frontispiece. Beginning with the June 2005 issue, the journal has been published on time. The median time from receipt to publication for manuscripts published in volume 117 was 374 days. The dates of publication for the issues of volume 117 were 19 April, 21 June, 14 September, and 15 December 2005. Except for the original submission of manuscripts, most correspondence and document transmittal between *The Wilson Bulletin* Editorial Office and authors, reviewers, and Allen Press was electronic. Design changes for the new *Wilson Journal of Ornithology* were completed in 2005.

I am grateful to Clait Braun, Richard Conner, Kathleen Beal, and Karl Miller, who served on the Editorial Board and reviewed numerous manuscripts. Kathy Beal offered statistical critiques of several manuscripts and compiled the index. Editorial assistants Beth Dillon, Alison Goffredi, and Cynthia Melcher performed essential editorial office operations including maintenance of the e-mail correspondence tracking system and the author/referee/manuscript database; corresponding with authors and reviewers; copy editing; and consulting with Allen Press, frontispiece artists, and other editors. I thank Allen Press, especially Karen Ridgway and Keith Parsons, for guidance and helpful advice on the final stages of the editorial and printing process. The U.S. Geological Survey Fort Collins Science Center has continued to be instrumental in its support of the editorial office.

The editorial office expenses, publication costs, and income for volume 117 (2005) were as follows: (1) Editorial Office expenses were $56,197 (salaries: $52,919; Editor's honorarium: $2,000; miscellaneous [office supplies, mailing]: $394; Editor's travel to 2005 WOS meeting: $883); (2) Publication costs (Allen Press) were $45,937.79; and (3) Income: authors paid $2,427.36 in page charges (403 manuscript pages were published for a mean author contribution of $6.02/page).

James A. Sedgwick, *Editor*

The reports of the standing committees are as follows:

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. The following library transactions occurred over the past calendar year:

Loans:

Loans of library materials to members involved 44 transactions to 13 members; these included 7 books loaned and 131 articles copied and scanned.

Acquisitions:

Exchanges: A total of 135 publications were received by exchange from 110 organizations or individuals.

Gifts: We received 28 publications from 25 organizations.

Subscriptions: We also received 34 publications from 23 subscriptions. We spent a total of $1,128.42 on subscriptions in 2005.

Donations: Members and friends donated 95 items. These donations included 1 book, 92 journal issues, and 1 translation.

Donors: The four members and friends donating materials include Joseph Jehl, Jr., Sharon Johnson, Edward H. Miller, and Tim Smart.

Purchases: New items purchased for $290.50 included 3 books and 54 journal issues.

Dispersals:

Gifts to other institutions: A total of 19 journal issues were donated to The Edward Grey Institute for Field Ornithology, Oxford, UK; 1,572 journal issues were sent to The Peregrine Fund library, for the cost of postage; and 147 journal issues were sent to the

Point Reyes Bird Observatory library, California, for the cost of postage.

Back issues: We sent out 79 back issues of *The Wilson Bulletin* for only the cost of postage.

Duplicates: We sold 21 duplicate books for $560.93.

Accessibility on the Web:

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Janet Hinshaw, *Librarian*

REPORT OF THE CONSERVATION COMMITTEE

In response to a request by WOS President, Doris J. Watt, the Conservation Committee was re-established in February 2006. Committee members currently include Daniel Klem, Jr., Joan L. Morrison, John A. Smallwood, and Douglas W. White. The committee will assess conservation issues, including those brought to it by Council, the membership, and the public at large. To accomplish this charge, the committee expects to solicit, as needed, input from those with expertise relevant to particular issues. The committee looks forward to working closely with the WOS Resolutions Committee, and to making recommendations for consideration by the WOS Council.

John Smallwood, *Chair*

The list of papers and posters presented at the NAOC meeting will be published in a supplement to *The Auk,* volume 124 (2007).

The Wilson Journal of Ornithology 118(4):593–594, 2006

REVIEWERS FOR VOLUME 118

Referees play a critical role in the editorial process. Thoughtful, incisive reviews are paramount in the maintenance of high scientific standards and journal quality. The following individuals completed and/or agreed to complete a review for me between 1 September 2005 and 31 August 2006 (referees who contributed two or more reviews appear in boldface). The Wilson Ornithological Society and the editorial staff of *The Wilson Journal of Ornithology* are deeply grateful to them for their assessments and recommendations.—James A. Sedgwick, Editor.

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Compiled by Rita A. Janssen and James A. Sedgwick

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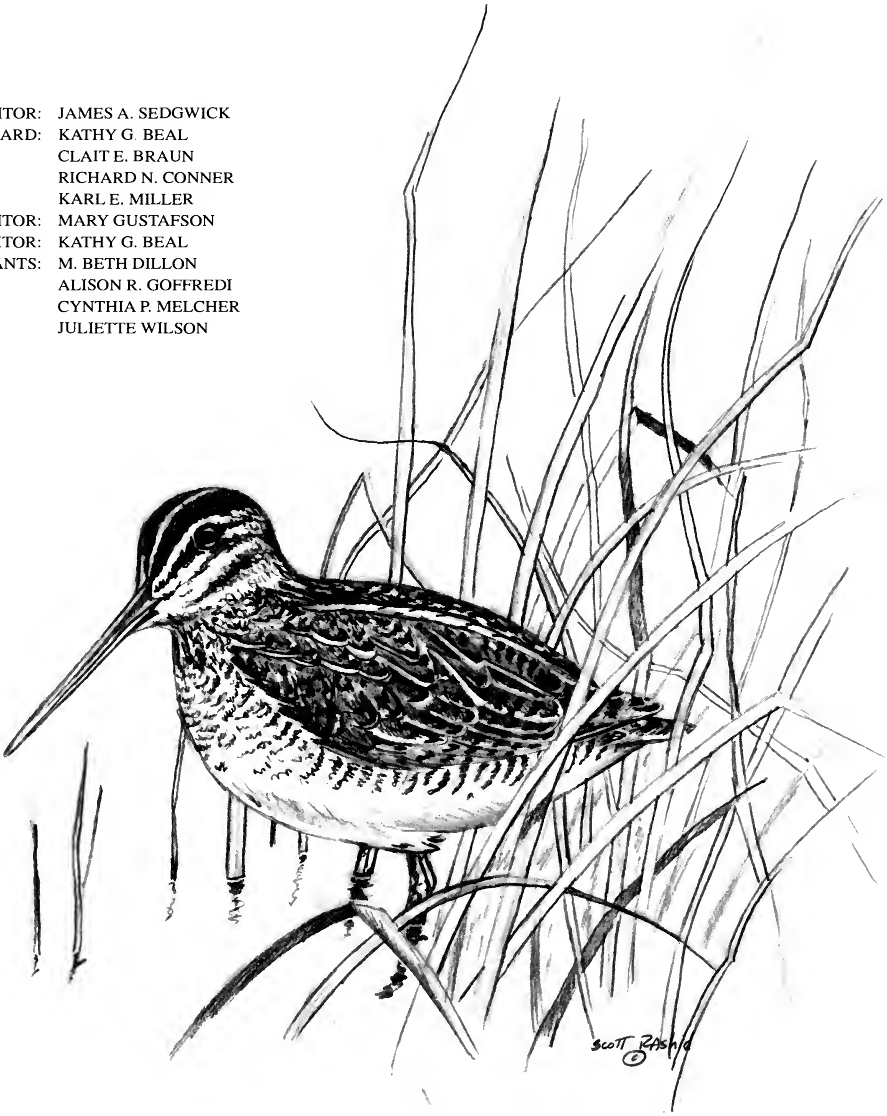
The Wilson Journal of Ornithology

Published by the Wilson Ornithological Society

Volume 118 *2006* *Quarterly*



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DATES OF ISSUE OF VOLUME 118 OF
THE WILSON JOURNAL OF ORNITHOLOGY

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NO. 2—5 JUNE 2006
NO. 3—22 SEPTEMBER 2006
NO. 4—27 DECEMBER 2006

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This issue of *The Wilson Journal of Ornithology* was published on 27 December 2006.

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