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FRONTISPIECE. Bicknell's Thrush (*Catharus bicknelli*) in its favored high-elevation, coniferous-forest habitat in the northeastern United States. Lambert et al. mapped the distribution of Bicknell's Thrush based on their model that predicts presence above an elevation threshold that decreases with increasing latitude. Original painting (acrylic and gouache) by Barry Kent MacKay.

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## A PRACTICAL MODEL OF BICKNELL'S THRUSH DISTRIBUTION IN THE NORTHEASTERN UNITED STATES

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STEVEN D. FACCIO,<sup>1</sup> AND JONATHAN L. ATWOOD<sup>2</sup>

**ABSTRACT.**—Bicknell's Thrush (*Catharus bicknelli*) is a rare habitat specialist that breeds in dense balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) forests at high elevations in the northeastern United States. Ongoing and projected loss of this forest type has led to increased demand for information on the species' status throughout the region. We used elevation, latitude, and forest type to construct a model of Bicknell's Thrush distribution in New York, Vermont, New Hampshire, and Maine. The model predicts the species to be present in conifer-dominated forests above an elevation threshold that descends with increasing latitude. The slope of the threshold ( $-81.63 \text{ m/}^{\circ}$  latitude) reflects climatic effects on forest composition and structure. The distribution model encompasses 136,250 ha of montane forest, including extensive areas of the White Mountains in New Hampshire and Adirondack Mountains in New York. To test model performance, we conducted point count and playback surveys along 1-km routes established in conifer forests above and below the threshold. The model accurately predicted the presence or presumed absence of Bicknell's Thrush on 61 of 72 routes (84.7%). When areas within 50 vertical m of the threshold were excluded, accuracy improved to 98.1%. The distribution model is a practical tool for conservation planning at local and regional levels. Potential applications include projecting effects of climate change on Bicknell's Thrush distribution, assessing risks of habitat alteration, and setting priorities for conservation and management. Received 9 February 2004, accepted 20 December 2004.

Bicknell's Thrush (*Catharus bicknelli*), once considered a subspecies of Gray-cheeked Thrush (*C. minimus*), gained full species status in 1995 (American Ornithologists' Union 1995). It has since been considered one of the most "at-risk" passerines in eastern North America. Partners in Flight (Pashley et al. 2000) ranks Bicknell's Thrush as the top conservation priority among Neotropical migrants in the Northeast, while the International Union for the Conservation of Nature (BirdLife International 2000) classifies the species as "vulnerable" on its list of threatened species.

Although there is no conclusive evidence of widespread population declines, reports of regional declines (Rompré et al. 1999, Rimmer et al. 2001b) and local extinctions (Christie 1993, Atwood et al. 1996, Nixon 1999, Lambert et al. 2001) have elevated concern for this rare species.

Bicknell's Thrush is a habitat specialist that occupies a naturally fragmented breeding range from the Catskill Mountains of New York to the Gulf of St. Lawrence and Cape Breton Island, Nova Scotia (Atwood et al. 1996, Rimmer et al. 2001a). It is the region's only endemic bird species. In New York, northern New England, and the nearby Estrie region of Québec, Bicknell's Thrush inhabits montane forests dominated by balsam fir (*Abies balsamea*), with lesser amounts of spruce (*Picea rubens* and *P. mariana*), white birch (*Betula papyrifera* var. *cordifolia*), and

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mountain ash (*Sorbus americana* and *S. decora*) (Atwood et al. 1996, Rimmer et al. 2001a, Connolly et al. 2002). Structural attributes of Bicknell's Thrush habitat include a dense understory of softwoods (Sabo 1980, Hale 2001, Pierce-Berrin 2001), low canopy height (Sabo 1980, Noon 1981, Hale 2001), and high incidence of snags, stumps, and dead fallen trees (Connolly 2000). These features typify chronically disturbed sites and regenerating fir waves (Sprugel 1976). Favorable habitat conditions for Bicknell's Thrush also may arise following disturbance by hurricane, ice storm, debris avalanche (Reiners and Lang 1979), or logging (Connolly 2000). Habitat suitability generally decreases with greater prominence of hardwoods (Sabo 1980, Noon 1981, Atwood et al. 1996, Hale 2001, Connolly et al. 2002); however, in the spruce-fir highlands of New Brunswick, Bicknell's Thrush inhabits both young conifer stands and regenerating hardwoods (Nixon 1996, Nixon et al. 2001).

Bicknell's Thrush also occurs in maritime spruce-fir forests at sites scattered along both shores of the St. Lawrence Seaway (Gauthier and Aubry 1996) and throughout the Gulf of St. Lawrence (Nixon 1999). Locations in the Gulf include the western tip of Anticosti Island, the Magdalen Islands (Gauthier and Aubry 1996), Cape Breton Island and small islands offshore of Cape Breton (Erskine 1992; D. Busby pers. comm.). Historic or sporadic records exist for several additional locations around the Bay of Fundy (Erskine 1992, Christie 1993).

In the northeastern United States, climate change could greatly reduce or eliminate balsam fir habitat as growing conditions become more favorable for hardwood species (Iverson and Prasad 2002). Over the long term, a shift in forest composition may impair the viability of Bicknell's Thrush populations in the region. Meanwhile, ski area expansion, communications tower construction, and wind power development incrementally reduce and fragment montane fir forests with unknown consequences for Bicknell's Thrush (Rimmer et al. 2001a). In order to conserve and properly manage remaining Bicknell's Thrush habitat, natural resource managers require reliable, site-specific occurrence information. Because it is not feasible to survey all potential habi-

tats, a predictive habitat map is required for effective conservation planning.

Wildlife habitat maps enable natural resource managers to identify suitable habitat and predict effects of management alternatives. When constructed in a geographic information systems (GIS) environment, such maps can be produced efficiently and applied consistently over large areas; however, the value of a GIS habitat model depends on its predictive capability. Therefore, model validation is a critical step in the habitat mapping process. Validation procedures yield measures of model performance that provide a basis for determining appropriate applications to research and management. An accurate GIS model is a flexible tool that focuses limited resources where they will have the greatest effect.

In a previous study, Atwood et al. (1996) identified forest type, latitude, and elevation as important factors underlying the distribution of Bicknell's Thrush in New England and New York. The goal of our study was to construct and test a predictive distribution model that incorporates forest type and accounts for the effect of latitude on the elevational occurrence of Bicknell's Thrush.

## METHODS

To investigate the effect of latitude on the elevational occurrence of Bicknell's Thrush, we examined records from distribution surveys of Bicknell's Thrush conducted between 1992 and 1995. In these surveys, Atwood et al. (1996) surveyed 443 locations across a wide range of elevations (0 to 1,451 m) in New York, Vermont, New Hampshire, and Maine. We plotted the elevation and latitude of each survey location, including those where Bicknell's Thrush was detected ( $n = 234$ ) and was not detected ( $n = 209$ ). If multiple individuals were observed during a survey, we plotted the lowest-elevation encounter. If no individuals were observed during a survey that spanned a range of elevations, we plotted the highest point surveyed.

Next, we used the Quantreg library in R (<http://lib.stat.cmu.edu/R/CRAN>) to estimate the 0.05 quantile regression (Cade and Noon 2003) of elevation as a linear function of latitude for locations where Bicknell's Thrush was observed. This produced an elevation

threshold above which 95% of the detections occurred. We then converted the linear threshold into an elevation mask, formed as a raster data set of  $30 \times 30$  m cells in ArcMap 8.2 (Environmental Systems Research Institute 2002). Cell values were calculated with the 0.05 quantile regression equation: elevation =  $-81.63(\text{latitude}) + 4,474.9$  m. Next, we laid the elevation mask over a digital elevation model of the northeastern United States (U.S. Geological Survey 1999). Summits, ridgelines, and slopes emerged above the mask as a vast complex of high-elevation habitat units. To identify potential Bicknell's Thrush habitat within these units, we mapped conifer-dominated stands. For this, we used forest composition data from the National Land Cover Data set, which classifies  $30 \times 30$  m cells based on canopy dominance (Vogelmann et al. 2001).

To test model performance, we conducted surveys between 2000 and 2002 on 53 mountains ( $>800$  m in elevation) not surveyed by Atwood et al. (1996). These mountains were scattered throughout the region and were selected based on availability of trails and volunteer observers. On each mountain, we established five survey stations, separated by 200 to 250 horizontal m, in areas dominated by conifers. Routes were designed to include the highest forested areas accessible by trail, often the summit, as well as adjacent ridges and slopes. Where conifer cover was limited, we located survey stations in mixed forests.

Trained technicians and volunteers performed point-count surveys under acceptable weather conditions (no precipitation, temperature  $>2^\circ$  C, wind speed  $<32$  km/hr) from 1 to 21 June. Surveys were conducted between 04:00 and 08:00 EDT, usually between 04:30 and 06:30. Observers listened quietly for 5 min, recording the number of Bicknell's Thrushes seen or heard at each station. They also recorded Bicknell's Thrushes seen or heard along the route, between survey stations. Observers who completed the route without detecting Bicknell's Thrush broadcast playbacks at each station on their way back to the starting point. Playbacks consisted of a 3-min, standardized recording of Bicknell's Thrush songs and call notes, followed by 2 min of silent listening. Playbacks were stopped upon first detection of the species.

Observers who completed the playback survey without encountering Bicknell's Thrush conducted follow-up, playback surveys at dusk or dawn before 15 July. This time, playback stations were located at 100-m intervals along the route. If no observations of Bicknell's Thrush were made during the second visit to a given site, the species was presumed to be absent. Observers conducted the full sampling sequence (point counts and up to two playback surveys, as needed) in at least 1 of the 3 years. Follow-up playbacks were not conducted at six locations that were  $>80$  m below the elevation mask. Atwood et al. (1996) surveyed 95 locations below this level without a confirmed encounter of Bicknell's Thrush.

Observers reported incidental encounters with Bicknell's Thrushes on 19 additional mountains not previously surveyed. These observations, made during one or more breeding seasons between 2000 and 2002, were added to the 53 original test routes for a total of 72 independent sample locations (New York:  $n = 34$ , Vermont:  $n = 19$ , New Hampshire:  $n = 16$ , Maine:  $n = 3$ ). Twenty-one of the 72 locations were within 50 vertical m of the elevation mask. Also during 2000–2002, with the same combination of systematic surveys and incidental sightings, we recorded the presence or presumed absence of Bicknell's Thrush on 130 mountains first sampled by Atwood et al. (1996) (New York:  $n = 30$ , Vermont:  $n = 56$ , New Hampshire:  $n = 26$ , Maine:  $n = 18$ ). Nineteen of 130 resampled locations occurred within 50 vertical m of the elevation mask. For model assessment, we used one elevation and one latitude value for each sample unit (1-km survey route or site of incidental encounter). At locations where Bicknell's Thrush was present, we calculated average elevation and latitude values based on all points of encounter. Where the species was not encountered, we calculated averages from the five survey stations.

We entered presence-absence data from new and resampled locations into separate error matrices (Table 1) and calculated a variety of accuracy measures (after Fielding and Bell 1997), including correct classification rate, sensitivity (proportion of true positives correctly predicted), specificity (proportion of true negatives correctly predicted), false pos-

TABLE 1. Error matrices for new Bicknell's Thrush survey locations and for resampled locations (first surveyed by Atwood et al. 1996), from 2000–2002 surveys.

Matrix		Observed present	Observed absent
New locations	Predicted present	56	10
	Predicted absent	1	5
Resampled locations	Predicted present	114	5
	Predicted absent	1	10

itive rate, false negative rate, positive predictive power, and negative predictive power. We also calculated prevalence, the proportion of locations at which Bicknell's Thrush was present. This variable affects the predictive power of species distribution models (Fielding and Bell 1997, Manel et al. 2001). Finally, we calculated Cohen's kappa, a statistic that measures the proportion of specific agreement after accounting for prevalence.

## RESULTS

Survey results from Atwood et al. (1996) show a strong, linear relationship between latitude and the lowest elevations occupied by

Bicknell's Thrush (Fig. 1). The lower limit of the species' distribution, as estimated by the 0.05 quantile regression, descends 81.63 m for every one-degree increase in latitude ( $\beta_1 = -81.63$ , 95% CI =  $-112.08$  to  $-38.13$ ;  $\beta_0 = 4,474.86$ , 95% CI =  $729.50$  to  $5,753.27$ ). The regression slope differed significantly from zero ( $H_0: \beta_1 = 0$ ) for this quantile (quantile rankscore test,  $P < 0.001$ ).

The elevation mask, developed in GIS from the 0.05 quantile regression, covers areas as high as 1,045 m in the Catskills ( $42^\circ$  N). In northern Maine ( $46.3^\circ$  N), areas as low as 695 m emerge above the mask. Throughout the region, 720 distinct land units occur above the

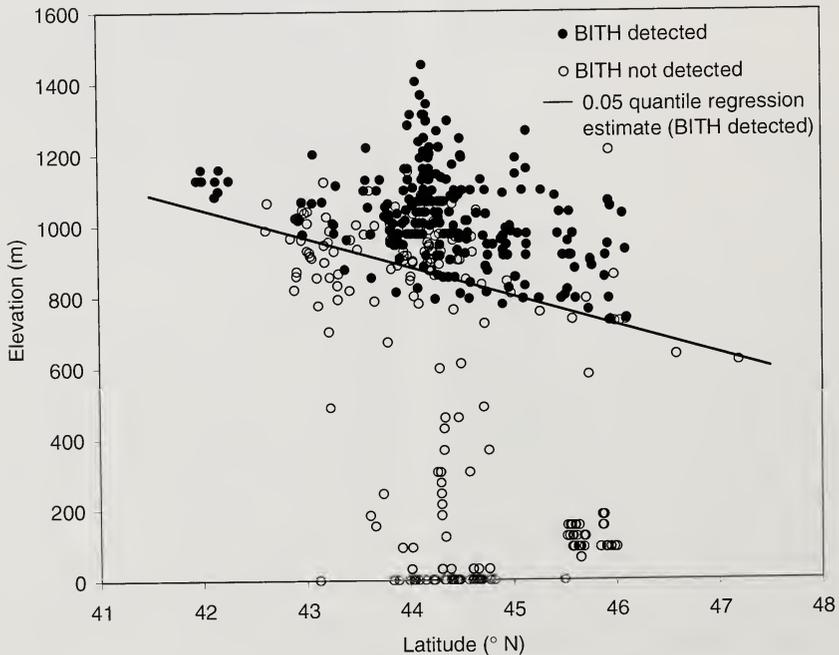


FIG. 1. Elevation and latitude of locations where Bicknell's Thrush (BITH) was detected ( $n = 234$ ) and not detected ( $n = 209$ ) during 1992–1995 surveys in the northeastern United States. Line is 0.05 quantile regression estimate of elevation as a linear function of latitude, incorporating only locations where Bicknell's Thrush was detected: elevation =  $-81.63$  (latitude) +  $4,474.9$  m.

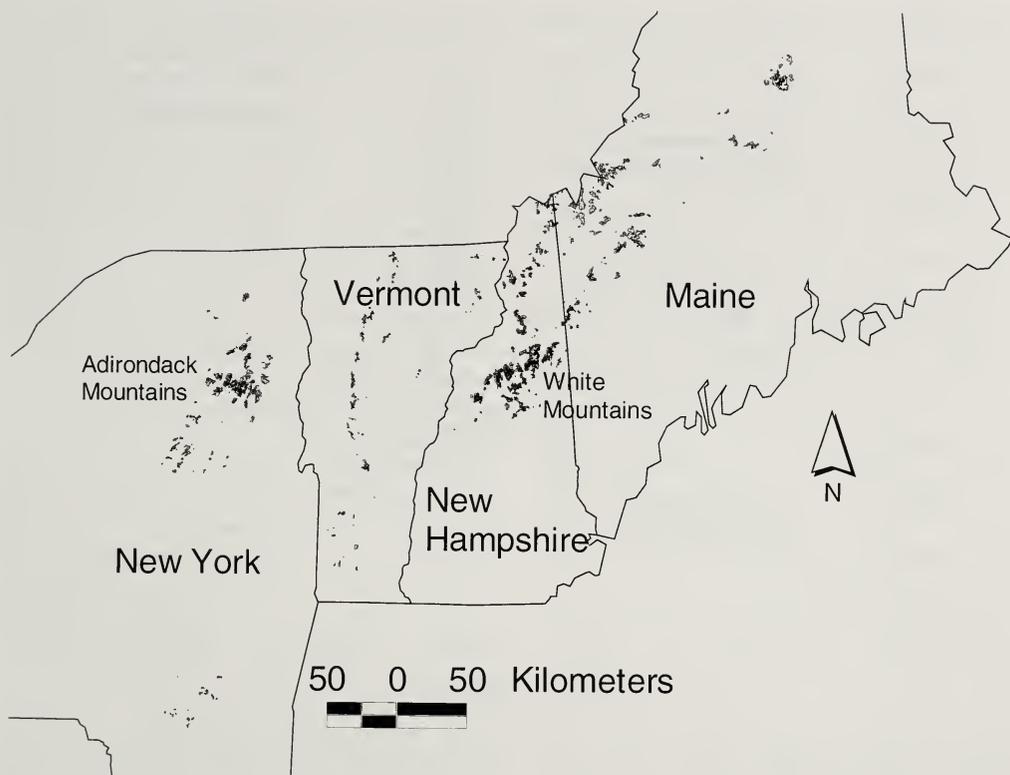


FIG. 2. Predicted distribution of Bicknell's Thrush in the northeastern United States. Shaded areas represent conifer forests (Vogelmann et al. 2001) above the model's elevation mask.

mask and contain 136,250 ha of conifer-dominated forest (Fig. 2), nearly all of which (99.7%) occurs in 387 units containing at least 5 ha of conifer—an amount sufficient to contain the average home range of a male Bicknell's Thrush (4.5 ha; Rimmer et al. 2001a). The average extent of conifer forest within the 387 units is 351.0 ha  $\pm$  56.8 SE, with highest values occurring in the White Mountains of New Hampshire and in the High Peaks region of New York's Adirondack Mountains. Of all states, New Hampshire has the most potential Bicknell's Thrush breeding habitat (59,024 ha; 43.4%), followed by Maine (33,662 ha; 24.7%), New York (31,985 ha; 23.5%), and Vermont (11,580 ha; 8.5%).

The Bicknell's Thrush distribution model correctly classified 61 of 72 locations (84.7%) that had never been surveyed for this species (Fig. 3, Table 2). Fifty-six of 57 occupied locations (98.2%) were correctly classified, compared with just 5 out of 15 (33.3%) unoccupied locations. Locations within 50 ver-

tical m of the elevation mask accounted for both errors of omission (false negatives) and 9 out of 10 errors of commission (false positives). The average, vertical deviation of misclassified locations from the elevation mask was 28.2 m  $\pm$  5.2 SE. When the 21 locations within 50 m of the elevation mask were excluded from the analysis, 51 of 52 locations (98.1%) were correctly classified.

The model correctly classified 124 of 130 locations (95.4%) first surveyed by Atwood et al. (1996). Four of the six errors occurred within 50 m of the elevation mask. When all new ( $n = 72$ ) and resampled ( $n = 130$ ) sites were combined, the model correctly classified 185 of 202 (91.6%) locations. Classification accuracy >50 m above and below the elevation mask was 98.8%, with 160 of 162 locations correctly classified.

Prevalence of Bicknell's Thrush was high among new locations (0.792) and resampled locations (0.877; Table 2). Cohen's kappa, which accounts for prevalence, measured

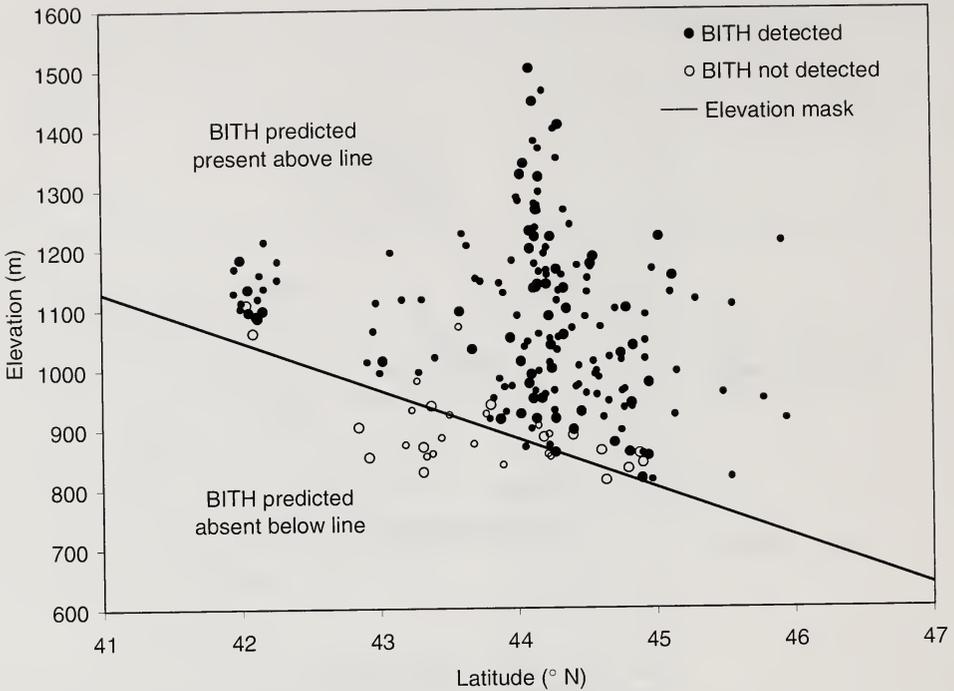


FIG. 3. Elevation and latitude of locations where Bicknell's Thrush (BITH) was detected ( $n = 172$ ) and not detected ( $n = 30$ ) during 2000–20002 surveys in the northeastern United States, shown in relation to elevation mask. Large circles represent new survey locations ( $n = 72$ ); small circles represent locations first surveyed by Atwood et al. (1996) and resampled for this study ( $n = 130$ ).

0.405 among new routes and 0.745 among resampled routes. Values of 0.4–0.6 indicate moderate model performance. Higher values (up to 1.0) are achieved when model performance ranges from substantial to perfect (after Landis and Koch 1977).

TABLE 2. Accuracy measures for Bicknell's Thrush distribution model. Values are calculated after Fielding and Bell (1997) with data from 72 new locations and from 130 (resampled) locations (2000–2002) first surveyed by Atwood et al. (1996).

	New locations	Resampled locations
Correct classification rate	0.847	0.954
Sensitivity	0.982	0.991
Specificity	0.333	0.667
False positive rate <sup>a</sup>	0.667	0.333
False negative rate <sup>b</sup>	0.018	0.009
Positive predictive power	0.848	0.958
Negative predictive power	0.833	0.909
Prevalence	0.792	0.877
Kappa	0.405	0.745

<sup>a</sup> Rate of commission error.

<sup>b</sup> Rate of omission error.

## DISCUSSION

The slope of the latitude-elevation relationship for Bicknell's Thrush occurrence ( $-81.63$  m/1° latitude) is nearly identical to the latitude-elevation relationship for treeline in the northern Appalachian Mountains ( $-83$  m/1° latitude); it also resembles that of the spruce-fir/deciduous forest ecotone ( $-100$  m/1° latitude; Cogbill and White 1991). The similarity in these slopes and the known association of Bicknell's Thrush with naturally disturbed forest stands suggest that the same factors governing stratification of mountain forest types regulate the availability of suitable habitat for Bicknell's Thrush. On a local scale, these include topography (slope shape, slope position, steepness, and aspect), substrate, and disturbance (Cogbill and White 1991). At regional and continental scales, temperature appears to be the primary, controlling factor (Wolfe 1979).

Cogbill and White (1991) found that the lower and upper spruce-fir ecotones were correlated with mean July temperatures of ap-

proximately 17° C and 13° C, respectively. If a warming climate were to elevate these isotherms, an upslope advance of hardwoods, and a corresponding loss of Bicknell's Thrush habitat might be expected. Tree-species distribution models project a major loss or extirpation of balsam fir habitat from the Northeast in four out of five climate change scenarios (Iverson and Prasad 2002). However, damage to hardwoods from ice- and snow-loading could moderate effects of climate change on forest composition at high elevations. The balsam fir's conical form allows it to shed snow more effectively than broad-branching hardwoods (Nykänen et al. 1997). Steep slopes might also provide refugia for balsam fir, which readily establishes in shallow, mineral soils (Frank 1990). Nevertheless, the persistence of Bicknell's Thrush in the Northeast may depend upon its ability to adapt to changing forest conditions.

A warming climate could enable mountain-top encroachment from species believed to be restricted to lower elevations by colder temperatures, including both a potential competitor of Bicknell's Thrush and a known pest of balsam fir. Swainson's Thrush (*Catharus ustulatus*) is a potential competitor (Noon 1981) whose distribution overlaps the lower reaches of Bicknell's Thrush habitat (Able and Noon 1976). A rise in summer temperatures could reduce separation between the two species by nullifying Bicknell's Thrush's greater tolerance for cold, considered by Holmes and Sawyer (1975) to confer a thermoregulatory advantage. Balsam woolly adelgid (*Adelges piceae*) is an exotic pest introduced from central Europe. It is currently controlled in the Northeast by cold winter temperatures, but has decimated stands of balsam fir in the southern Appalachians (Iverson et al. 1999).

The mechanisms by which a warming climate might affect Neotropical migrants are numerous and largely unpredictable, although even small changes could have far-reaching effects on productivity and survivorship (Rodenhouse 1992). Susceptibility to extinction is high for species like Bicknell's Thrush that occupy restricted and patchy habitat within small ranges (Huntley et al. 1997). In recent decades, extirpations of Bicknell's Thrush have occurred at coastal locations in Canada (Tufts 1986, Christie 1993, Nixon 1999) and

along the southern periphery of the species' breeding range (Atwood et al. 1996, Lambert et al. 2001). Although there is no evidence for a link to climate change, the observed pattern is consistent with range shifts attributed to global warming in other animal species (Parmesan and Yohe 2003, Root et al. 2003). Our model of Bicknell's Thrush habitat provides the opportunity to predict changes in the species' distribution under different climatic conditions. Information gained through this exercise might be used to develop strategies to mitigate anticipated habitat loss.

Overall, the distribution model achieved high measures of classification accuracy, positive predictive power, and negative predictive power (Table 2). However, such levels can be achieved by chance alone where the prevalence of a species is high (Olden et al. 2002), as it was in this study. Cohen's kappa provides a measure of improvement over chance that places prediction success in perspective (Fielding and Bell 1997, Manel et al. 2001). The kappa values we calculated for new routes (0.406) and resampled routes (0.745) correspond with moderate and substantial model performance, respectively. An improved test of the model, including low and middle elevations, would almost certainly yield higher kappa values because more locations would be correctly classified as unoccupied. By concentrating sampling effort at high elevations, we limited the interpretive value of this statistic.

The model's predictive success was nearly perfect at locations >50 m above or below the elevation mask (Fig. 3). By comparison, error rates were high within 50 m of the mask, where hardwoods become scarce and conifers achieve dominance. Able and Noon (1976) described this band as a principal distributional limit for songbirds on northeastern mountains and measured its breadth as approximately 100 m in the Adirondack and Green mountains. Cogbill and White (1991) provided a similar measure (87 m) for the average breadth of the deciduous forest/spruce-fir ecotone in the Adirondack and northern Appalachian mountains. Our findings are consistent with these measures and verify this boundary as an important factor in organizing avian community structure across four degrees of latitude.

Low densities of Bicknell's Thrush may have resulted in reduced detectability at some locations, particularly during silent counts (Penteriani et al. 2002). Even playbacks can fail to elicit detectable responses from Bicknell's Thrush (Nixon et al. 2001), which may exhibit agonistic postures in dense vegetation rather than vocalize (Noon 1981). Indeed, the failure to detect Bicknell's Thrush at many apparently suitable sites during the 1990s may indicate sampling error. Such error could have resulted from limited sampling (a single visit to 80 locations) and a relatively loose time-frame for broadcasts ("usually within three hours of sunrise or sunset"; Atwood et al. 1996). The possibility of error during model testing (2000–2002) was reduced by multiple visits and strict broadcast guidelines. The higher frequency of detection above the elevation mask, compared with the results of Atwood et al. (1996), provides evidence of improved methodology.

Accuracy rates vary widely among habitat-relationship models that have been tested for songbirds (e.g., 20–33%, Bart et al. 1984; 60–90%, Rice et al. 1986; 53–93%, Kilgo et al. 2002). Models constructed for habitat specialists are more likely to generate accurate predictions than those developed for generalists (Kilgo et al. 2002). This presents conservation planning opportunities for rare species with narrow habitat requirements, like Bicknell's Thrush. Our model of Bicknell's Thrush distribution can be used as a practical tool to guide research, stewardship, and land protection initiatives in the mountains of New York and northern New England. Specific applications include: identification of monitoring and research sites, reserve design, recreational planning, regulatory review and impact assessment (as for tower construction or ski area expansion), and assignment of management responsibility to specific landowners.

To evaluate tradeoffs in each of these applications, it is important to consider the significance of model error. In general, excessive commission error may result in undue expenditure of limited resources at marginal sites, while excessive omission error may result in failure to identify important, occupied sites. Fortunately, GIS provides the flexibility to adjust the Bicknell's Thrush elevation mask to achieve an acceptable ratio between these two

types of error. Such adjustments can be made according to project resources and objectives. For example, a risk-averse strategy to protect Bicknell's Thrush habitat might lower the elevation mask to identify all potential breeding areas, including those along the lower spruce-fir ecotone. Though sparsely populated by Bicknell's Thrush, this zone is extensive in mountainous landscapes and could contribute substantially to overall numbers (Hale 2001). A research initiative seeking to maximize encounters with the species might take a more selective approach and raise the mask.

For projects that seek information on the status of Bicknell's Thrush at sites within 50 m of the elevation mask, we recommend the use of playback surveys in June and early July. Six or more visits may be required to detect all individuals in a given year (Nixon et al. 2001). If initial attempts to verify presence fail, additional effort is advised in at least 2 successive years or until presence is confirmed. Repeat surveys will reduce errors associated with low density (i.e., low detectability) and irregular occupancy of marginal sites. Our own repeat surveys confirm their value. Since 2003, we have observed Bicknell's Thrush at 6 of 15 locations where it was predicted to occur, but was not detected during model assessment (Vermont Institute of Natural Science [VINS] unpubl. data).

The model's estimate of Bicknell's Thrush habitat in the Northeast (136,250 ha) falls within the previously published range of values derived from land cover and land area above the 915-m contour line (100,000 to 150,000 ha; Atwood et al. 1996). However, the addition of latitude as a variable eliminates areas in southern portions of the range once thought suitable for Bicknell's Thrush and adds sites at northern latitudes once considered too low. Despite this important advance, the model does not distinguish early- to mid-successional or stunted forests from tall stands, which are of lesser importance to the species. Extensive surveys (Noon 1981, Hale 2001; VINS unpubl. data) and intensive, radio-telemetry studies (VINS unpubl. data) indicate that Bicknell's Thrushes make little use of large patches of mature, montane conifer that lack well-developed shrub and subcanopy layers. Nonetheless, such stands may be just an ice storm, fir wave, or hurricane away from

developing the structural characteristics of suitable habitat. Likewise, the habitat value of a young forest sheltered from disturbance may diminish over time.

Conservation and mitigation strategies should recognize that the location of suitable habitat patches shifts due to the dynamic nature of forests at high elevations. Rather than focus at the stand level, a prudent long-range approach would treat the entire unmasked area as the management unit. Such an approach would benefit other species that nest in montane forests of the Northeast, such as Black-backed Woodpecker (*Picoides arcticus*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Blackpoll Warbler (*Dendroica striata*), and White-winged Crossbill (*Loxia leucop-tera*).

We advise caution in the application of this model north of 45° N latitude. Unmasked areas in this region include >40,000 ha of managed timberland in Maine (VINS unpubl. data), some of which occurs as mixed, regenerating forest. The Canadian Wildlife Service has documented use of this forest type by breeding Bicknell's Thrushes in highland regions of Québec (Y. Aubry pers. comm.), New Brunswick (Nixon 1996), and Nova Scotia (D. Busby pers. comm.). Furthermore, model testing in northern Maine was limited, allowing for the possibility that Bicknell's Thrush occurs at lower elevations than predicted by the model. Such a possibility is supported by Wolfe's (1979) treeline model, which slopes gradually from 20° N to about 45° N and then begins to steepen. Cogbill and White's (1991) models of Appalachian Mountain ecotones maintain their linear shape until about 47° N, where the relationship between elevation and the spruce-fir/deciduous ecotone changes to a steeper slope. Records of Bicknell's Thrush at low elevations in Québec (175–1,160 m; Ouellet 1993), New Brunswick (450–700 m; Nixon et al. 2001), and Nova Scotia (<175 m; D. Busby pers. comm.) underscore the need for further model testing in northern Maine.

The absence of evaluation sites below the mask in the Catskills (42.0–42.5° N) is of less concern. We are confident that the model is sufficiently inclusive in this area, since it captures virtually all of the region's upland spruce-fir.

Recently developed and evolving modeling techniques will enable construction of regional models of habitat importance for Bicknell's Thrush, based on topographic and lithographic features (Banner 2002), remotely sensed forest physiognomy (Hale 2001), and/or landscape structure (Hale 2001, Lambert et al. 2002). Incorporation of abundance data into more sophisticated models will permit reasonable estimates of population size and provide a benchmark for establishing range-wide population objectives. However, construction and validation of such models will require considerable time and resources. Though basic in its parameters and predictions, the current model is accurate and effective for most applications. It is built from elevation and land cover data that are widely available, inexpensive, consistent across state boundaries, and easily updated. Furthermore, it depicts habitat over a major portion of the species' range. Together, these qualities make it a practical tool for conservation planning.

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## OFFSHORE MARINE OBSERVATION OF WILLOW PTARMIGAN, INCLUDING WATER LANDINGS, KUSKOKWIM BAY, ALASKA

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**ABSTRACT.**—We report an observation of Willow Ptarmigan (*Lagopus lagopus*) encountered 8 to 17 km from the nearest shoreline on Kuskokwim Bay, Alaska, on 30 August 2003. The ptarmigan were observed flying, landing on our research vessel, and landing and taking off from the water surface. We also report on one other observation of ptarmigan sitting on the water surface and other marine observations of ptarmigan from the North Pacific Pelagic Seabird Database. These observations provide evidence that Willow Ptarmigan are capable of dispersing across large bodies of water and landing and taking off from the water surface. *Received 19 July 2004, accepted 4 January 2005.*

Willow Ptarmigan (*Lagopus lagopus*) have a Holarctic distribution and are found throughout much of Alaska, typically occupying alpine and arctic tundra (Hannon et al. 1998). In contrast to the residential habits of most other grouse species (Gruys 1993, Hannon et al. 1998), Willow Ptarmigan are known to make seasonal migrations that may cover distances of several hundred kilometers. Although their wing morphology and muscle composition suggest that they are better adapted to longer migrations and sustained flight than other galliforms (Drovetski 1996), galliforms generally are considered to have limited ability for sustained flight (Tobalske et al. 2003). For Willow Ptarmigan, migration between breeding and wintering habitats typically occurs in early fall, with return migration occurring in spring (Hannon et al. 1998); Gruys (1993) reported that Willow Ptarmigan migrating from summer to winter habitats moved in flocks of up to 200 birds. Ptarmigan, upland birds not commonly associated with water, normally do not swim or dive (Hannon et al. 1998), but Dixon (1927) observed a Willow Ptarmigan wade into shallow creek water to forage on insects, and Hannon et al. (1998) report that 1-day-old chicks can swim if they fall into water.

Because ptarmigan are not usually associ-

ated with water and generally exhibit limited flight endurance, it is not clear whether ptarmigan would be able to migrate long distances over bodies of water. Determining the extent of this ability may be a key element to understanding dispersal patterns and population structure. Rock Ptarmigan (*L. muta*) breeding on the Aleutian Islands, for example, are characterized by genetic divergence among major island groups with little gene flow between island populations (Holder et al. 2000, 2004). Holder et al. (2000) further pointed out that no inter-island movement of individual ptarmigan has ever been reported, although the distances between islands are often less than those covered by migrations of inland ptarmigan.

On 30 August 2003, during a survey for pelagic juvenile salmon in Kuskokwim Bay, Alaska (60° 0' N, 162° 15' W), we encountered a group of 100 to 125 Willow Ptarmigan. We observed the ptarmigan for approximately 2 hr (08:00 to 10:00 Alaska Standard Time) as we cruised south along the 162° 16' W longitude line. We first encountered the ptarmigan when we were approximately 8 km from shore. Our track was roughly parallel to the east coast of Kuskokwim Bay and distance to shore ranged from 8 to 17 km. Initially, two ptarmigan (a female and male) landed on our vessel and rested for approximately an hour before flying away. Over the next hour (09:00–10:00), approximately 125 birds repeatedly flew around the vessel. A few landed on the vessel and rested for short periods (<15 min) before flying off in the distance and returning to the vicinity of the boat (Fig.

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FIG. 1. Willow Ptarmigan in flight, on a research vessel, and on the water, Kuskokwim Bay, Alaska, 30 August 2003. See additional photographs at [www.absc.usgs.gov/research/Fisheries/Western\\_Alaska/ptarmigan.htm](http://www.absc.usgs.gov/research/Fisheries/Western_Alaska/ptarmigan.htm).

1). All birds appeared to be exhausted after landing on the vessel, exhibiting rapid breathing with open beaks. At least 10 ptarmigan were observed landing on the water surface, resting (<10 min), then taking off from the water surface. When we encountered the ptar-

migan, the sea was calm, winds were light, and the sky was overcast. The nearest weather station, at Cape Newenham on the southern boundary of Kuskokwim Bay and approximately 120 km from our location, reported calm winds, visibility of 16 km, and an air temperature of 13°C (Federal Aviation Administration automated weather monitoring station).

To determine whether other ptarmigan had been observed at sea or landing on water, we queried the North Pacific Pelagic Seabird Database ([www.absc.usgs.gov/research/NPPSD/](http://www.absc.usgs.gov/research/NPPSD/)), which contains pelagic seabird survey data collected over the last 30 years in the North Pacific Ocean, Bering Sea, and adjacent waters. Of 57 ptarmigan records—including 16 Willow Ptarmigan, 6 Rock Ptarmigan, and 35 unidentified ptarmigan—all were associated with shorelines of the Chuckchi Sea, Arctic Ocean, or Norton Sound, Alaska. Only 1 ptarmigan was sitting on the water, 12 were not classified according to behavior, 12 were flying in a consistent heading, 9 were flying below the crests of waves or swells (suggesting flight over water), 2 were bathing, 15 exhibited courtship behavior (likely terrestrial observations), and 6 were sitting or standing followed by flushing (likely terrestrial observations). Of the behaviors reported, 12 appear to have been associated with water, including sitting on water, bathing, or flying below wave crests. The single record of a ptarmigan sitting on the water was of a Rock Ptarmigan observed on 26 June 1976 at Kasegaluk Lagoon (68° 51' N, 165° 50' W), adjacent to the Chukchi Sea.

It is not clear why the ptarmigan we observed on Kuskokwim Bay were flying offshore. Since the weather was calm at the time and had been so for several days, it is unlikely that this group had been displaced by wind. Willow Ptarmigan are common on the coastal plain adjacent to Kuskokwim Bay and typically migrate in September—from the coastal plain to mountains in the east (approximately 90 km; M. Rearden pers. comm.). It seems likely that the ptarmigan we encountered had gathered as they migrated from breeding habitats on the coastal plain to wintering habitats.

Given the distribution of ptarmigan on offshore islands, such as the Aleutian Islands, Alaska, it is not unlikely that dispersal occurs

over water. Understanding the dispersal capabilities and patterns of animals is a critical step in examining population structure and metapopulation dynamics (Weins 1996). Dispersal among islands is regulated by the dispersal capabilities of a species and the distance between islands. Our observation of Willow Ptarmigan on Kuskokwim Bay and the observation of Rock Ptarmigan at Kasegaluk Lagoon are the first records of ptarmigan not only landing and sitting on the water surface, but also successfully taking off after resting on the water surface. These observations add to our understanding of dispersal by ptarmigan and may provide insight concerning dispersal of ptarmigan across large bodies of water.

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## MINIMUM POPULATION SIZE OF MOUNTAIN PLOVERS BREEDING IN WYOMING

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**ABSTRACT.**—As human disturbance of natural landscapes increases, so does the need for information on declining, threatened, and potentially threatened native species. Proposed listing of the Mountain Plover (*Charadrius montanus*) as threatened under the U.S. Endangered Species Act in 1999 was found unwarranted in 2003, but this species remains of special concern to management agencies and conservation groups. Whereas large concentrations of breeding Mountain Plovers occur in Montana and Colorado, estimates of the numbers of Mountain Plovers in Wyoming have ranged from only 500 to 1,500 individuals and are based largely on conjecture. In 2002, we visited all known breeding locales in the state to define areas of concentrated sightings in the Laramie, Shirley, Washakie, Great Divide, and Big Horn basins. In 2003, we used distance sampling to estimate breeding bird densities in these five areas. We pooled these estimates and applied the resulting density to a minimum occupied range for the Mountain Plover based on the documented sightings and a previously derived home-range size of  $56.6 \text{ ha} \pm 21.5 \text{ (SD)}$  to generate a minimum population estimate for the state. Average Mountain Plover density was  $4.47 \pm 0.55 \text{ (SE)}$  birds/km<sup>2</sup>. We calculated a minimum population estimate of 3,393 birds for Wyoming. The Mountain Plover population breeding in Wyoming appears to contribute substantially to a revised continental population estimate of 11,000 to 14,000 birds. Our approach may have applications to quantifying minimum population status of other uncommon species or species of special conservation concern using current database records, such as those compiled in Natural Heritage Programs at the state level. Received 28 January 2004, accepted 10 December 2004.

The Mountain Plover (*Charadrius montanus*) is one of 12 avian species endemic to the grasslands of North America (Mengel 1970). Plovers nest on the shortgrass prairie and shrub-steppe of the western Great Plains and Colorado Plateau, especially in areas used historically by large assemblages of herbivores, such as prairie dogs (*Cynomys* spp.), bison (*Bison bison*), and pronghorns (*Antilocapra americana*; Knopf 1996a). The species winters from north-central California to Arizona, Texas, and northern Mexico.

Once numerous in Colorado and Wyoming and common in western Kansas, South Dakota, and Nebraska, Mountain Plovers began to decline throughout their range early in the 20th century (Laun 1957). They have continued to do so over the past 30 years at a rate approximating 3% per year (Knopf 1996a). As a result, the species' continental breeding range has been significantly reduced. Today the majority of the Mountain Plover's breed-

ing range is restricted to east-central Montana (Skaar 2003), the tablelands of Wyoming (Oakleaf et al. 1992), and eastern Colorado (Andrews and Righter 1992, Kingery 1998). The North American population was recently estimated at 8,000 to 10,000 birds (Knopf 1996a).

In response to evidence of the species' widespread decline, in 1999 the U.S. Fish and Wildlife Service (USFWS) proposed listing the Mountain Plover as threatened under the U.S. Endangered Species Act (ESA) (U.S. Fish and Wildlife Service 1999). The USFWS recently determined that threats to Mountain Plovers and their habitat are not likely to endanger the species in the foreseeable future; thus, the proposed listing of the bird was withdrawn (U.S. Fish and Wildlife Service 2003). Regardless, the Mountain Plover remains as a species of special concern to wildlife and land managers throughout its range.

Although significant breeding populations occur in Montana and Colorado, there is evidence that Wyoming may provide habitats for many breeding Mountain Plovers as well. Survey efforts for plovers in Wyoming, especially in the wake of the recent ESA proposal, have revealed pockets of breeding birds throughout the state, particularly in south-central and eastern Wyoming. The contribution of Moun-

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tain Plovers in Wyoming to the continental breeding population is poorly understood, as no reliable statewide population estimate exists. Rough estimates, based largely on conjecture, have ranged from 500 to 1,500 individuals (FLK).

Wunder et al. (2003) recently estimated the size of a similarly undefined population of Mountain Plovers in South Park, (Park County), Colorado. Distance sampling was used to estimate density of breeding plovers, from which a population estimate was extrapolated based on an estimate of occupied habitat. Plovers in South Park occurred at an average density of  $7.9 \pm 0.9$  (SE) birds/km<sup>2</sup> across sampled portions of >80,000 ha of potential habitat. Wunder et al. (2003) concluded that South Park, with an estimated population of >2,300 Mountain Plovers, contributes 15–20% of breeding plovers to the continental population.

Following the success of Wunder et al. (2003) in generating a population estimate in South Park, Colorado, we used distance sampling to generate density estimates of breeding plovers in Wyoming. Although we used distance sampling following Wunder et al. (2003), plovers are much more widely scattered in fragmented habitats across Wyoming compared with their single-county study in Colorado. Our objectives were to (1) compile all documented sightings of Mountain Plovers in Wyoming, (2) visit all locals of documented sightings in 2002 to confirm presence of breeding plovers, (3) conduct surveys of adult plovers at selected areas in 2003, and (4) extrapolate plover densities over the documented breeding range to obtain a minimum population estimate for Mountain Plovers in Wyoming.

## METHODS

*Documented sightings and statewide reconnaissance.*—We collected information about documented locations of Mountain Plovers from state and federal agencies, non-profit and consulting firms, and individuals in Wyoming. We mapped these locations using a Geographic Information System (GIS; ESRI ArcMap 8.3). More than 40 agencies, firms, and individuals contributed to the compiled database representing the documented distribution of Mountain Plovers throughout the state.

Between 12 May and 18 July 2002, we visited all locations in Wyoming with one or more pre-2002 plover sightings and surveyed for presence of Mountain Plovers. We modeled survey protocol after Mountain Plover survey guidelines set forth by the USFWS (U.S. Fish and Wildlife Service 2002). We drove transects along established roads and two-track roads, stopping at 0.4-km intervals to conduct visual scans for plovers. We conducted these scans outside of the vehicle to prompt movement of nesting or resting plovers and maximize their detectability. There was no predetermined length of time for each visual scan; rather, each lasted as long as necessary to cover a 360-degree panorama around the vehicle. Surveys were conducted in the morning between local sunrise and 11:00 MST, and in the afternoon between 16:30 and local sunset to take advantage of horizontal lighting that facilitates detection of plovers. Playback calls were not used. GPS coordinates were taken at the site where each Mountain Plover was first observed. As time allowed, we also surveyed surrounding areas of acceptable habitat from which there were no prior records of plovers; these new sightings were added to the pre-2002 database.

*Mountain plover study areas.*—We identified five Mountain Plover breeding areas for our study. We stratified these areas into two grassland landscapes and three desert-shrub landscapes. The two grassland landscapes were located in the Laramie and Shirley basins, and the desert-shrub areas were in the Big Horn, Great Divide, and Washakie basins. The five areas were selected based upon accessibility for field personnel and the availability of adequate potential habitat to find a minimum of 40 plovers in a 5-day survey period. Accessibility was limited on many privately owned lands and occasionally vehicle access was limited on public lands.

Study areas in the Laramie and Shirley basins included a portion of the Laramie Plains that extends north and west from Laramie to Medicine Bow and Foote Creek Rim, and the central portion of Shirley Basin, roughly delineated by the two intersections of Wyoming highways 77 and 487 in northeastern Carbon County. These basins represent the highest-elevation grasslands in Wyoming (Knight 1994) and are characterized by interspersed short-

and mixed-grass prairie. Shortgrass species include blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*). Commonly occurring mixed-grass species include needle-and-thread grass (*Stipa comata*), western wheatgrass (*Agropyron smithii*), Sandberg bluegrass (*Poa sandbergii*), threadleaf sedge (*Carex filifolia*), and Indian ricegrass (*Oryzopsis hymenoides*). Several shrub species, including pricklypear cactus (*Opuntia polyacantha*), big sagebrush (*Artemisia tridentata*), budsage (*A. spinescens*), and fourwing saltbush (*Atriplex canescens*) are present. Vegetation communities vary with topography, which ranges from basins and salt pans to elevated plateaus. White-tailed prairie dog (*Cynomys leucurus*) colonies are common and grazing by domestic cattle and pronghorn antelope is pervasive.

The desert-shrub study areas included the Mexican Flats, located west of Dad between Wamsutter and Baggs in the Washakie Basin (Carbon County); a portion of the Great Divide Basin of the Red Desert located south of Cyclone Rim in northern Sweetwater County; and parts of the Big Horn Basin near Cody and Powell (Park County) and Greybull (Big Horn County), particularly Polecat and Chapman benches. These shrubland areas are typified by saline soils and are dominated by greasewood (*Sarcobatus vermiculatus*), shadscale (*Atriplex confertifolia*), fourwing saltbush, and Gardner's saltbush (*A. gardneri*), with winterfat (*Ceratoides lanata*) and pricklypear cactus interspersed. A mosaic is often formed with stands of big sagebrush, saltbush, and greasewood. Mixed-grass species such as western wheatgrass, prairie junegrass (*Koeleria macrantha*), saltgrass (*Distichlis stricta*), and needle-and-thread grass also occur. Community composition is highly dependent on topography, moisture availability, and soil type. Oil and gas development is common, particularly in the Mexican Flats area. The landscape is grazed by domestic sheep and cattle, and by pronghorn. Wild horses are also present in the Washakie and Great Divide basins to the south. White-tailed prairie dog colonies are common throughout.

**Population sampling.**—During two 10-day surveys in 2003, we surveyed for adult Mountain Plovers at the five study areas defined in 2002. The initial survey occurred in late May,

when most breeding birds were on nests. This survey was designed to detect all adult plovers, but especially those that ultimately might nest unsuccessfully and leave the area before the second survey. The second survey occurred in late June to coincide with the chick-rearing phase. The courtship phase in late April and early May was avoided, as survey estimates from that period would be subject to error incurred by detections of migrating birds.

Using an ATV driven at  $\leq 15$  km/hr, two observers conducted surveys in each study area along transects with a minimum of 400-m spacing between lines. Plovers move evasively in response to observers on foot, but are more tolerant of slow-moving vehicles; thus, we used an ATV to help ensure detection of birds at their initial location. Each transect began on a road or two-track that ran alongside (narrow strips) or through (large patches) potential plover habitat. We used a random numbers table to determine the distance (from the access road or two-track) driven into each survey area before beginning the transect perpendicular to the access road. We stopped at 0.4-km intervals while surveying and stepped off the ATV. This approach encouraged plovers to stand from their nests, and thus become more visible. All transects were conducted simultaneously by two observers (the double-observer method). Playback calls were not used. We used a laser range finder (Bushnell Yardage Pro Sport, rated to 450 m) to measure the distance to each bird detected and a standard compass to establish the sighting angle from the transect line. We took GPS coordinates on the transect line for each detection. We conducted all sampling between local sunrise and 11:00 and between 16:30 and local sunset to take advantage of horizontal lighting (reducing the effects of plumage counter-shading) and peak activity levels of the birds. We further reduced the sampling window on exceptionally warm days ( $>30^{\circ}$  C) when heat may have reduced activity levels and heat waves may have reduced detectability. Sampling was not conducted when inclement weather or poor lighting threatened to bias probability of detection.

**Occupied range.**—To define the known occupied range for Mountain Plovers in Wyoming, we combined Mountain Plover loca-

tions from the reconnaissance phase in 2002, the distance-sampling phase in 2003, and the locations documented elsewhere. We then overlaid onto the GIS map a lattice with grid size equal to the average home range of the Mountain Plover during brood rearing (56.6 ha). The average home-range size of 56.6 ha was first determined from a study in Weld County, Colorado, by affixing radio transmitters to adult plovers that were attending chicks, and recording daily movements (Knopf and Rupert 1996). Comparable home-range sizes have since been found in other Mountain Plover habitats (Dreitz et al. 2005). We calculated the minimum breeding range of Mountain Plovers in Wyoming by summing the area of the grids in the overlaid lattice that intersected at least one Mountain Plover location. A minimum estimate of population size for Wyoming was based on the 2003 density estimates extrapolated across this minimum breeding range.

*Distance analyses.*—Using program DISTANCE 3.5 (Thomas et al. 1998), we estimated overall Mountain Plover densities, as well as densities for subsets of grassland and desert-shrub habitats. Distance sampling (Buckland et al. 2001) uses a set of robust models to estimate densities on the basis of measured distances between detected objects and a central point or transect from which the objects were detected. With regard to underlying assumptions, methodological self-assessment, and efficiency in the field, DISTANCE is superior to relative-abundance estimates generated using point counts (Norvell et al. 2003). We treated the distance data as continuous estimates and considered each of six models suggested by Buckland et al. (2001). These models were each composed of a key function or general shape proposed to fit the detection function, and a nonparametric flexible form called a “series expansion” that adjusted the key function. The six models used were the uniform key function with cosine and simple polynomial expansion series, the half-normal key function with cosine and hermite polynomial expansion series, and the hazard-rate key function with cosine and simple polynomial expansion series. The uniform and half-normal key functions are proposed shapes for the detection function, based on *a priori* assumptions about the detection pro-

cess, whereas the hazard-rate key function is a derived model. We pooled plover sightings recorded from the two 2003 surveys and truncated the largest 10% of sampled distances to reduce error incurred by outliers, as recommended by Buckland et al. (2001). Histograms of the probability of detection were inspected for violation of statistical assumptions. We also considered the six suggested models with stratification by habitat, but stratified models were inferior to unstratified models. Comprehensive explanations of sampling procedure and model selection are given in Buckland et al. (2001) and Burnham and Anderson (2002). Our analytic approach was similar to that used by Wunder et al. (2003) for estimating Mountain Plover densities in Park County, Colorado.

We used Akaike’s Information Criterion (AIC) to evaluate the relative strength of each of the 12 models. Because AIC identifies the best of a set of competing models but does not reflect the quality of fit, goodness-of-fit *P*-values were also considered to identify poorly fitting models ( $P < 0.05$ ), should any exist.

To avoid bias incurred by basing parameter estimates on a single model from a set of closely competing models, we used model averaging based on weighted AIC contributions from all 12 models to generate overall density estimates. We estimated density, detection probability, and detection strip half-width for grassland and desert-shrub habitat subsets using model averaging across a set of unstratified models for each habitat.

## RESULTS

*Inventory and occupied range.*—We compiled and mapped >2,000 sightings of Mountain Plovers representing input from >40 sources. These records included 1,347 sightings from the Wyoming Natural History Diversity Database, ~93% and ~57% of which were reported in the last 20 and 10 years, respectively. Virtually all documented sightings from other sources were made within the last 10 years. In 2002, we detected 171 Mountain Plovers on 1,416 km of roads and two-tracks during reconnaissance visits to previously documented sites. We added these 2002 plover locations and 449 new locations recorded during distance sampling in 2003 to the database of documented sightings to map the

TABLE 1. Estimates (SE) of Mountain Plover density, probability of detection, and effective detection strip half-width in grassland and desert-shrub habitats in Wyoming for 2003. Estimates (SE) are derived from DISTANCE 3.5 (Thomas et al. 1998).

	Grassland	Desert-shrub
Birds detected	113	190
Density (plovers/km <sup>2</sup> )	5.17 (1.06)	4.23 (0.67)
Detection probability	0.82 (0.13)	0.73 (0.06)
Effective strip half-width (m)	114.70 (18.68)	111.50 (8.6)

known occupied range of Mountain Plovers in Wyoming. The resulting 2,695 compiled observations intersected 1,341 cells in the overlaid 56.6-ha "home range" grid. Therefore, the known occupied range of Mountain Plovers in Wyoming included at least 75,901 (i.e.,  $1,341 \times 56.6$ ) ha of potential habitat. The five study areas for the randomized distance sampling in 2003 overlapped 44% of the known plover locations in Wyoming.

*Density and minimum population estimates.*—We detected 303 Mountain Plovers during distance sampling along 276 km of transects, roughly divided among the five study areas in 2002. Pooled data across the two 2003 sampling efforts yielded a minimum of 40 detections for each study area. Estimates of density, detection probability, and effective strip half-width were similar for grassland and desert-shrub habitats (Table 1).

Although the hazard-rate key function with cosine and simple polynomial expansion series provided the best fit to the detection function for the unstratified data, all 12 models (six unstratified, six stratified) had  $\Delta AIC \leq 5.0$  and goodness-of-fit  $P$ -values  $> 0.1$ . The overall density estimate, averaged over 12 models, was  $4.47 \pm 0.55$  birds/km<sup>2</sup> (Table 2). In general, the unstratified models showed lower AIC values than the stratified models. Although the poorest fitting unstratified model was as likely as the best stratified model ( $\Delta AIC = 2.2$ ,  $w_i = 0.07$  for both), the unstratified models contributed 78% of the weighted estimates. All of the models fit the data well: goodness-of-fit test statistics for the unstratified models (from lowest to highest  $P$ -value) ranged from  $\chi^2 = 3.56$  ( $P = 0.17$ ) to  $\chi^2 = 2.12$  ( $P = 0.35$ ).

Assuming an average home-range size of

TABLE 2. Models used to generate density estimates for Mountain Plovers in five breeding areas in Wyoming for 2003. Both pooled and stratified models are included. Models were run using 303 detections and 10% truncation. Models are ordered by increasing  $\Delta AIC$ . The AIC weight ( $w_i$ ), density estimate, and coefficient of variation (CV) are provided for each model.

Model	$\Delta AIC$	AIC weight ( $w_i$ )	Density (birds/km <sup>2</sup> )	CV
<b>Unstratified</b>				
Hazard rate + cosine	0.0 <sup>a</sup>	0.20	4.37	0.12
Hazard rate + simple polynomial	0.0 <sup>a</sup>	0.20	4.37	0.12
Uniform + simple polynomial	0.6	0.15	4.60	0.11
Half normal + hermite polynomial	1.7	0.09	4.45	0.15
Half normal + cosine	2.2	0.07	4.53	0.15
Uniform + cosine	2.2	0.07	4.52	0.14
<b>Stratified<sup>b</sup></b>				
Uniform + simple polynomial	2.2	0.07	4.59	0.10
Hazard rate + simple polynomial	3.0	0.05	4.37	0.12
Hazard rate + cosine	3.0	0.05	4.37	0.12
Half normal + hermite polynomial	4.2	0.02	4.80	0.11
Half normal + cosine	4.2	0.02	4.80	0.11
Uniform + cosine	5.0	0.02	4.55	0.11

<sup>a</sup> AIC = 2692.7

<sup>b</sup> Stratified by habitat type.

56.6 ha (Knopf and Rupert 1996) for Mountain Plovers, the overall density estimate can be applied to the 75,901 ha of geographic range documented in Wyoming to generate a population estimate of 3,393 birds (75,901 ha  $\times$  4.47 birds/km<sup>2</sup>). The lower confidence limit for average Mountain Plover home range (35.1 ha) can be used to generate a more conservative estimate of 2,270 birds. Because the occupied range for Mountain Plovers in Wyoming is surely underestimated, the upper confidence limit for home range (78.1 ha) may be a better approximation, yielding a population estimate of 4,427 birds.

### DISCUSSION

Generating reasonable population estimates is particularly challenging for low-density species of conservation concern, such as the Mountain Plover. Distance sampling is a powerful tool for developing such estimates given the time and resources to collect adequate data. Buckland et al. (2001) recommend a sample size of at least 60–80 detections, but admit that suitable precision may require several hundred detections. Reasonable sample sizes were only achieved in this study by focusing sampling efforts on areas with relatively high concentrations of recent (<20 years) Mountain Plover sightings. Those areas occur either where plovers are most visible or where people look for plovers. Much (perhaps most) of the potential plover habitat in Wyoming has never been surveyed for the species.

The validity of the extrapolated minimum population estimates described here largely rests on the accuracy of estimates of occupied range and average home-range size for Mountain Plovers. Given the impracticality (scale of effort, access to private lands) of surveying all potential Mountain Plover habitat in Wyoming, we initially considered a habitat-based model that employed satellite imagery for estimating the occupied range of the species. This model was deemed unsuitable because Mountain Plovers in Wyoming frequently occupy habitat patches of such small size or subtle distinction, relative to the dominant cover type, that suitable patches cannot be distinguished remotely. Therefore, we compiled documented sightings of plovers collected by field biologists to represent a best-available approximation of a statewide survey for

Mountain Plovers. It is likely that many breeding locales are still unknown and unsurveyed, thus affirming the *minimum* nature of our estimates. The second assumption, that the home-range size from Weld County, Colorado, can be applied to other areas, has recently been confirmed by studies that revealed comparable home-range size in dissimilar habitats at various locales (Dreitz et al. 2005). Finally, we assumed that densities in sampled areas are representative of densities throughout the species' occupied range. This latter assumption was supported by the similar plover densities calculated in grassland versus desert-shrub habitats.

We did not need to assume plover occupancy of all pre-2003 grid cells in our extrapolation of calculated plover density across the pre-2003 sightings template. Distance sampling in the 2003 survey areas was independent of both the pre-2003 cell distribution and any knowledge of statewide plover-density patterns. The 2003 distance-sampling transects (covering 44% of the pre-2003 area) would have been as likely to sample 2003-occupied as 2003-unoccupied cells in the pre-2003 database. Thus, the distance sampling effort in 2003 included "occupancy" information relative to the earlier sightings.

Plover densities were comparable across habitat types. The overall density in grassland habitats was slightly higher (5.17 birds/km<sup>2</sup>) than in desert-shrub habitats (4.23 birds/km<sup>2</sup>), with considerable overlap between confidence intervals. Eighty-six percent of the desert-shrub confidence interval was contained by the grassland confidence interval. The congruence of density estimates across habitats supports the calculation of a pooled density estimate to represent plover habitats statewide.

The average density of Mountain Plovers in documented breeding areas in Wyoming (4.47  $\pm$  0.55 birds/km<sup>2</sup>) is somewhat lower than most density estimates within the species' breeding range. Finzel (1964) reported 6.2 birds/km<sup>2</sup> near Laramie and 12.3 birds/km<sup>2</sup> near Cheyenne, Wyoming. Wunder et al. (2003) reported densities of 6.0–9.0 birds/km<sup>2</sup> for South Park, Colorado, and Knopf (1996a) reported densities of up to 4.7 birds/km<sup>2</sup> on Pawnee National Grassland in Colorado and 1.3–6.8 birds/km<sup>2</sup> on prairie dog towns in Montana. Graul and Webster (1976) estimated

plover densities at 8.0 birds/km<sup>2</sup> in areas of Wyoming and Montana.

Our calculated potential habitat of 759 km<sup>2</sup> for Mountain Plovers in Wyoming is an underestimation. Most private lands have never been surveyed for plovers. These lands are primarily used for grazing, a major component of plover habitats throughout the year (Knopf 1996a, Wunder and Knopf 2003). The only desert regions of Wyoming being surveyed consistently at present are those targeted for oil and gas leasing or development. We also note that whereas the most productive grazing lands in Wyoming are in private ownership, our surveys were conducted on publicly owned, less productive landscapes. Mountain Plover densities are likely higher in the privately owned and more productive landscapes, and those landscapes are under-represented in our potential-habitat database.

Considering that the recent global population estimate for Mountain Plovers is 8,000 to 10,000 individuals (Knopf 1996a), and that Wyoming's conservative estimate of 3,393 plovers may not include birds that (1) occupy large expanses at low densities, (2) occur in isolated small patches of habitat (e.g., historic buffalo wallows; FLK pers. obs.), or (3) breed at undiscovered spots, Wyoming's Mountain Plovers appear to contribute substantially to a revised continental population estimate of 11,000 to 14,000 birds. Furthermore, management strategies for Mountain Plover habitat in Wyoming often emulate the historical ecological drivers (e.g., drought and grazing; Knopf and Samson 1997) to a greater extent than do practices in neighboring states where cultivation and urbanization are more widespread. When rangeland conversion to row cropping does occur in Wyoming, it is generally to a lesser extent than in other states within the plover's range. Between 1982 and 1997, more than three times as much rangeland within the occupied breeding range of Mountain Plovers was converted in Montana than in Wyoming; 12 times as much potential habitat was converted in Colorado (U.S. Fish and Wildlife Service 2003). Wyoming's population of Mountain Plovers and relatively intact expanses of grazed rangeland may become increasingly important for the species as urban and agricultural development continues in contiguous states.

Mountain Plovers, like many species of conservation interest, occur in low densities and in a variety of landscapes. Plovers often are not detected in general biotic surveys due to their relative inconspicuousness. Our study took advantage of an existing database of mostly casual observations to focus intensive surveys for estimating population status in Wyoming. This approach may be useful for quantifying minimum population size of other species of conservation concern. Existing database records, such as those available from state Natural Heritage Programs, may be particularly useful.

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## NEST SURVIVAL RELATIVE TO PATCH SIZE IN A HIGHLY FRAGMENTED SHORTGRASS PRAIRIE LANDSCAPE

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**ABSTRACT.**—Understanding the influences of habitat fragmentation on vertebrate populations is essential for the protection and ecological restoration of strategic sites for native species. We examined the effects of prairie fragmentation on avian reproductive success using artificial and natural nests on 26 randomly selected, privately owned patches of shortgrass prairie ranging in size from 7 to 454 ha within a cropland matrix in Washington County, Colorado, summer 2000. Survival trends of artificial and natural nests differed. Daily survival of artificial nests increased with patch size up to about 65 ha and differed little at larger patch sizes, whereas daily survival of Lark Bunting (*Calamospiza melanocorys*) and Horned Lark (*Eremophila alpestris*) nests decreased with increasing size of the grassland patch. We hypothesize that our unexpected findings of lower survival of natural nests with increasing patch sizes and different trends between artificial and natural nests are due to the particular structure of predator communities in our study area and the ways in which individual predators respond to artificial and natural nests. We recommend that the value of small habitat patches in highly fragmented landscapes not be overlooked. Received 1 April 2004, accepted 3 November 2004.

Understanding the influences of habitat structure and habitat fragmentation on the viability of grassland species is essential to conservation planning, especially for protection and ecological restoration of strategic sites for native species. Many grassland bird species, including those of the shortgrass prairie, have experienced population declines in the past 3 decades (Knopf 1994, Murphy 2003, Sauer et al. 2003). Between 1966 and 2002, populations of Lark Buntings (*Calamospiza melanocorys*) and Horned Larks (*Eremophila alpestris*) declined 2.0 and 1.6% per year, respectively, in the High Plains physiographic region (Sauer et al. 2003). Although mechanisms for these declines have not been identified, factors influencing reproductive success are among the possibilities. Shortgrass is the least disturbed of the three prairie types in North America, with as much as 40% remaining unplowed (Samson and Knopf 1996). Even though the extent of habitat loss is considerably less than in the tallgrass prairie (82–99%; Samson and Knopf 1996), habitat loss and fragmentation of breeding areas may contribute to population declines of shortgrass prairie birds.

Broad generalizations regarding the negative effects of habitat fragmentation on density and reproductive success of avian species are common in the scientific literature of the past 2 decades (Ambuel and Temple 1983, Herkert 1994, Donovan et al. 1995, Freemark et al. 1995). Studies on the effects of habitat fragmentation, specifically patch size and isolation, initially were stimulated by island biogeography theory (MacArthur and Wilson 1967, Diamond and May 1981) and subsequently by emerging landscape perspectives (Fahrig and Merriam 1994, Wiens 1995). When detected, patch size effects typically show that smaller habitat patches have lower habitat quality, more edge habitat, fewer species, fewer or no individuals of area-sensitive species, and/or lower reproductive output—due to increased predation and brood parasitism or decreased food abundance (Brittingham and Temple 1983, Herkert 1994, Burke and Nol 1998, Robinson 1998). These generalities are now being incorporated as assumptions in quantitative models of the effects of habitat fragmentation and edge effects on the demography of birds (Donovan and Lamberon 2001, Bollinger and Switzer 2002).

Despite broad support for these generalities, inconsistencies have been documented in well-studied systems. Although larger forest patches in forested landscapes are thought to provide better habitat (Donovan et al. 1995, Robinson et al. 1995, Thompson et al. 2002), not all studies support that pattern (Marzluff

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and Restani 1999). For example, in western forests, predation rates in fragments are often lower than in unfragmented sites (Tewksbury et al. 1998, Cavitt and Martin 2002). Current paradigms are rapidly evolving with the increased scrutiny of inconsistencies in the forest fragmentation literature (Donovan et al. 1997, Walters 1998, Marzluff and Restani 1999, Heske et al. 2001, Thompson et al. 2002). A major challenge to our understanding of the effects of habitat fragmentation on birds is the variability in their responses to fragmentation, or “differential sensitivity” (Walters 1998)—across regions, landscapes, habitats, species, and populations.

The effects of prairie fragmentation on reproductive success of grassland birds have been documented primarily in tallgrass prairie and in artificial nest studies. The effects are equivocal. Several bird species have experienced lower nest success in smaller grassland patches or near woody edges in field-forest ecotones (Herkert et al. 2003), but such effects do not universally apply to all grassland habitats and species (Gates and Gysel 1978, Johnson and Temple 1990, Winter and Faaborg 1999, Winter et al. 2000). Of five studies that employed artificial nest techniques in grasslands, only one (Burger et al. 1994) reported increased mortality of artificial nests with decreasing grassland patch size and distance from edges (in this case forest edges). Four of these studies reported no differences in mortality of artificial nests relative to grassland patch size or distance to edge, including forested and agricultural edges (Mankin and Warner 1992, Clawson and Rotella 1998, Pasitschniak-Arts et al. 1998, Howard et al. 2001). The lack of a patch size effect in these studies may result, in part, from the range in patch sizes being above or below a threshold at which an effect could be detected.

The search for generalities is often a search for clear and consistent trends reported by several studies. “Similar conclusions obtained from studies of the same phenomenon conducted under widely differing conditions will give us greater confidence in the generality of those findings than would any single study” (Johnson 2002). To contribute to our knowledge of potential effects of prairie fragmentation on birds, we conducted a study in a highly fragmented shortgrass prairie land-

scape (<15% grassland). The primary objective of our study was to determine the effects of patch size on reproductive success of prairie birds. We selected our study sites randomly so that we could make inferences to our entire target population (see *Site selection*) rather than just to the individual grassland patches.

## METHODS

*Study area.*—The shortgrass prairie landscape is dominated by xeric grasses, such as buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). Common breeding birds are Horned Larks, Western Meadowlarks (*Sturnella neglecta*), Lark Buntings, Chestnut-collared Longspurs (*Calcarius ornatus*), and Grasshopper Sparrows (*Ammodramus savannarum*). Potential mammalian predators of ground-nesting birds include thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), coyotes (*Canis latrans*), swift foxes (*Vulpes velox*), long-tailed weasels (*Mustela frenata*), badgers (*Taxidea taxus*), and striped skunks (*Mephitis mephitis*). Common snake species that opportunistically prey on birds include bullsnakes (*Pituophis melanoleucus*), western hognose snakes (*Heterodon nasicus*), and prairie rattlesnakes (*Crotalus v. viridis*).

Our study was conducted during the summer of 2000 in a 4,842-km<sup>2</sup> agricultural region of Washington County in northeastern Colorado (39° 34' N to 40° 27' N; 102° 48' W to 103° 28' W). Land-use cover types in the study area include dryland wheat (non-irrigated wheat production in a 2-year rotation system; 73.9%), shortgrass prairie rangeland (14.3%), Conservation Reserve Program (CRP) fields (6.1%), and irrigated crops (3.7%). This agricultural area was adjacent to three large grasslands, totaling 1,689 km<sup>2</sup>, that were not considered in this study.

*Site selection.*—We used satellite imagery (provided by the Colorado Division of Wildlife) to quantify land cover and restricted randomization to select study sites. Using Arc-Info, we identified all ( $n = 557$ ) polygons of short- and midgrass prairie and measured corresponding area and perimeter. We calculated a diversity index ( $DI$ ; Patton 1975) as

$$DI = \frac{TP}{2\sqrt{A\pi}}$$

where  $TP$  is the total perimeter of the polygon and  $A$  is the area of the polygon. For reference, a circle has a  $DI$  of 1 and a square has a  $DI$  of 1.3. Of the 557 identified grassland polygons, the median area was 35.7 ha (mean =  $125.5 \pm 367.6$  SD; range 2.1–4,886.8 ha) and mean  $DI = 2.0 \pm 0.7$  SD. We omitted 96 polygons with  $DI > 2.5$  to eliminate the potentially confounding effect of highly elongated patches.

We sorted the polygons into several size classes (in increments of 10 ha between 0 and 150 ha, and in increments of 50 ha between 150 and 500+ ha) and randomly selected 2–4 from each size class as possible study sites. We ground-truthed the polygons (hereafter grassland patches) to verify their size and isolation and to update the surrounding land-use type. We considered only grassland patches that were at least 0.4 km from other grassland habitats. Grassland patches that were within 0.4 km of human habitation or riparian trees were also omitted to minimize the effects of predation by farm cats or corvids (Delisle and Savidge 1996). We obtained permission from landowners and conducted our study on 26 grassland patches ranging from 7 to 454 ha in size (mean =  $106.4 \pm 109.4$  SD, CV = 1.03;  $n = 4$  patches 7–20 ha,  $n = 6$  patches 21–50 ha,  $n = 7$  patches 50–100 ha,  $n = 5$  patches 100–200 ha,  $n = 4$  patches >200 ha).

**Artificial nests.**—Nests consisted of a scrape on the ground where we placed two fresh Japanese quail (*Coturnix japonica*) eggs and one clay egg (mean =  $22 \times 15$  mm,  $n = 20$ ) made of soft modeling compound (Sculpey III brand) to approximate the size of Lark Bunting eggs (mean =  $22 \times 17$  mm; Baicich and Harrison 1997). Clay eggs aided in the identification of nest predators (by examining tooth impressions) and enabled us to record predation by predators too small to handle quail eggs (i.e., small rodents; Major and Kendal 1996). We inserted an orange-painted nail in the ground under the eggs to facilitate locating the nests after a disturbance. Artificial nests ( $n = 312$ ) were set out at 24 sites between 31 May and 3 June and at 2 additional sites on 8 June 2000. At each site, we placed six nests near an edge (a grassland/fallow-field interface at 18 sites and a grassland/planted-field interface at 8 sites; planted sites were primarily wheat). At 100-m intervals

along the edge, we paced a random distance (5–30 m) toward the interior and placed the artificial nest. We also placed six nests in the interior of each site (generally 100–500 m from the edge). In small sites, interior nests were placed as far from the edge as possible; 95% of all interior nests were  $\geq 100$  m from an edge and only one interior nest was  $< 75$  m. Interior nests were also placed 100 m apart; however, nests were placed closer together in small sites (50 m in four and 25 m in one) to enable the placement of six nests. Distance from the patch edge averaged  $17.9$  m  $\pm 7.1$  for edge nests and  $259.1$  m  $\pm 121.1$  for interior nests. For nest survival analyses, we coded distance from edge as 1 = edge, 2 = interior.

We checked nests twice, at 5 and 9 days after placement; eggs were removed from disturbed nests at the first check and from all remaining nests during the second check. Nests were classified as intact or disturbed based on signs of disturbance to either quail or clay eggs. Nests were considered disturbed if quail eggs were missing, broken, or moved, or if clay eggs were missing, moved, or had tooth impressions. We classified markings on the clay eggs as rodent, non-rodent, insect, or unknown by comparing them with known tooth impressions made from skulls in the zoology collection at Colorado State University, Fort Collins. In the absence of other signs of disturbance, nests containing clay eggs with only insect marks were considered intact.

**Natural nests.**—All grassland patches were systematically searched for nests by dragging a rope between two observers  $\sim 28$  m apart and by observing adult behavior. We marked the location of nests with unmarked wooden stakes ( $2.9 \times 28.5$  cm) positioned 10 m from nests; painted wooden stakes ( $2.9 \times 28.5$  cm) were also placed 30 m from nests (aligned with the unmarked stake and nest) to facilitate relocating nests. When nests were found, we floated two eggs to determine their age, using a technique described by Westerskov (1950) and modified for Lark Buntings and Horned Larks. We monitored the nests and recorded numbers, ages, and status of eggs and nestlings at 2- to 4-day intervals until nests were empty. During the last nest check, we noted signs that would help determine whether young fledged (parents feeding young or call-

ing in the vicinity, fecal droppings outside of the nest [deposited only when young hop out; AAYA pers. obs.]. For each nest, we estimated distance from patch edge, coded as 1: <30 m, 2: 30–100 m, and 3: >100 m.

*Vegetation sampling.*—Vegetation structure and composition of grassland patches were characterized by sampling between 31 May and 7 June at six random points along line transects through the center of each site. Measurements included visual estimates of the percent cover of grasses (identified to species), sedges, forbs, shrubs, cacti, and bare ground within 5-m radius plots, as well as measurements of grass height and vegetation density at distances of 1, 3, and 5 m due east from the point. Vegetation density was recorded as the total number of vegetation hits on a 1-cm-diameter pole at intervals of 0–5, 5–10, 10–20, and 20–30 cm above ground. We constructed a variable (VegStruc) to describe overall vegetation structure as percent cover of green vegetation  $\times$  median grass height  $\times$  vegetation density.

*Analyses.*—We used Pearson correlation to assess relationships between patch area (ln-transformed to improve normality) and nine vegetation-structure variables: percent cover of grasses, forbs, shrubs, bare ground, and green vegetation (grasses, sedges, forbs, shrubs, and cacti); maximum grass height; median grass height; vegetation density; and overall vegetation structure.

We used the “Mayfield logistic regression” approach recently described by Hazler (2004) to examine daily survival of artificial and natural nests as a function of three variables: patch size (Patch area), distance from edge (Edge), and vegetation structure (VegStruc). Mayfield logistic regression is an alternative to typical logistic regression (i.e., 1 nest = 1 trial) because it accounts for the number of exposure days (i.e., 1 exposure day = 1 trial). We used the “Last Active-B” approach of Manolis et al. (2000) to calculate exposure days, and we censored the last nest check interval for nests with unknown fate (Stanley 2004). During nest checks after the fledge date, we assumed nests were successful if we observed fledglings, parental behavior near nests that suggested presence of fledglings (calling, feeding young), or fecal droppings immediately outside the nest.

We fitted models with PROC LOGISTIC (SAS Institute, Inc. 1999) and evaluated these models using AIC (Akaike 1973, Burnham and Anderson 2002) corrected for small sample size (AIC<sub>c</sub>). The difference ( $\Delta_i$ ) between model  $i$  and the model with the minimum AIC<sub>c</sub> value allows for a quick comparison and ranking of models. The model with the smallest AIC<sub>c</sub> is the best-approximating model of the candidate models, given the data. The AIC<sub>c</sub> weight ( $w_i$ ) for model  $i$ , calculated as

$$\frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)}$$

(where  $R$  is the number of candidate models in the set), is useful in assessing the weight of evidence in favor of a model. Burnham and Anderson (2002:167) recommend the use of summed Akaike weights ( $\sum w_i$ ) to evaluate the relative importance of variables when a balanced model set is used (e.g., in our analysis each variable appeared in four models). We computed a relative importance measure for each variable by summing Akaike weights over every model in which that variable appeared.

Because of model-selection uncertainty (it is plausible that models with  $\Delta\text{AIC}_c$  values <7 are reasonable), we model-averaged the SAS-generated effect sizes ( $\hat{\beta}$ , regression coefficients) over the entire set of models with a weighted average based on Akaike weights (Burnham and Anderson 2002:253, equation 5.8). We computed unconditional standard errors for the effect sizes, thereby incorporating model-selection uncertainty into precision estimates, and used the  $Z$  distribution to calculate 95% confidence intervals (CI). Because PROC LOGISTIC models nest failure, signs of all coefficients were reversed to interpret effects on survival (see Hazler 2004). Herein we present a positive  $\beta$  to indicate increased nest survival and a negative  $\beta$  to indicate decreased nest survival relative to a given predictor variable. The strength of the effect ( $\hat{\beta}$ ) is indicated by whether the 95% CI of the regression coefficient includes zero. A 95% CI where  $\hat{\beta}$  does not overlap zero is analogous to  $P < 0.05$ , and a 90% CI where the  $\hat{\beta}$  does not overlap zero is analogous to  $P < 0.10$ .

TABLE 1. Summary of model-selection results for survival of artificial and natural nests (Lark Bunting and Horned Lark) in Washington County, Colorado, summer 2000. Models with the lowest  $\Delta AIC_c$  and the greatest Akaike weight ( $w_i$ ) have the most support and are highlighted in boldface.  $K$  is the number of parameters in each model, including the intercept and each explanatory variable;  $n$  = total number of trials (nest-exposure days).

Nest survival models	Artificial nests ( $n = 1,492$ )			Lark Bunting ( $n = 204$ )			Horned Lark ( $n = 321$ )		
	$K$	$\Delta AIC_c$	$w_i$	$K$	$\Delta AIC_c$	$w_i$	$K$	$\Delta AIC_c$	$w_i$
Patch area <sup>a</sup> + Edge + VegStruc	5	1.61	0.138	4	3.99	0.056	4	3.94	0.039
Patch area <sup>a</sup> + Edge	4	1.63	0.137	3	1.96	0.155	3	1.89	0.110
Patch area <sup>a</sup> + VegStruc	4	<b>0.00</b>	<b>0.308</b>	3	2.04	0.149	3	1.78	0.116
Edge + VegStruc	3	4.83	0.027	3	6.18	0.019	3	4.11	0.036
Patch area <sup>a</sup>	3	0.09	0.294	2	<b>0.00</b>	<b>0.414</b>	2	<b>0.00</b>	<b>0.282</b>
Edge	2	6.44	0.012	2	4.59	0.042	2	2.10	0.099
VegStruc	2	3.30	0.059	2	4.22	0.050	2	2.33	0.088
Constant	1	5.05	0.025	1	2.58	0.114	1	0.40	0.231

<sup>a</sup> We used a quadratic function of patch area in artificial nest models; patch area was used in Lark Bunting and Horned Lark models.

We ln-transformed patch area (hereafter patch area) to improve normality. Because we were unsure of the shapes of curves describing relationships between nest survival and patch area, we compared AIC values of models that included (1) patch area and (2) a quadratic function of area (patch area + patch area<sup>2</sup>) before formalizing the candidate models. We then ran all possible additive combinations, including a constant model, for a total of eight models.

We present calculated estimates of overall nest survival, artificial nest survival for each grassland patch, and natural nest survival in small (<80 ha) and large (>80 ha) patches using the Mayfield technique (Mayfield 1975) and standard errors of the estimates following Johnson (1979). We used the 80-ha cutoff to ensure adequate sample sizes for Mayfield estimates of natural nest survival. Overall nest success was calculated as the daily survival rate (DSR) raised to the power of the length of the nesting period (21 and 20 days for Horned Larks and Lark Buntings, respectively). All estimates are reported  $\pm$  SE, unless noted otherwise.

## RESULTS

*Vegetation composition and structure.*—The dominant grasses in the study sites, in order of percent cover, were buffalograss, western wheatgrass (*Agropyron smithii*), blue grama, needleandthread (*Hesperostipa comata*), sixweeks fescue (*Vulpia octoflora*), and red threeawn (*Aristida purpurea*). Median

grass height was 10.0 cm and ranged from 1 to 20 cm across all patches. There were no differences in vegetation structure that related to patch area; none of the nine vegetation structure variables was correlated with patch area ( $|r| < 0.270$ ,  $P > 0.15$  in all cases). The matrix immediately surrounding the grassland patches was primarily dryland wheat (approximately 78% of patch perimeter), CRP monocultures of smooth brome (*Bromus inermis*, 18%), and irrigated crops (4%).

*The influence of grassland patch size on predation rates on artificial nests.*—Mean daily survival of artificial nests across all sites was  $0.834 \pm 0.010$  (95% CI = 0.815–0.853,  $n = 312$ ). Edge nests had slightly greater daily survival than interior nests ( $0.841 \pm 0.013$ ; 95% CI = 0.815–0.867,  $n = 156$  edge nests; and  $0.826 \pm 0.014$ ; 95% CI = 0.799–0.853,  $n = 156$  interior nests).

For artificial nests, we chose the quadratic rather than the linear function of patch area to represent area in the candidate models, based on relative  $AIC_c$  values of 1339.35 and 1343.75, respectively. Daily survival of artificial nests was best explained by the quadratic function of patch area and VegStruc (Table 1). Distance from edge had little influence on survival of artificial nests, as denoted by low Akaike model weights (Tables 1, 2). The predictor variables ordered by their estimated importance are area, vegetation structure, and edge, as portrayed by the summed weights ( $\Sigma w_i$ ) of 0.876, 0.532, and 0.314, respectively (Table 2).

TABLE 2. Survival of artificial nests increases with a quadratic function of patch area, up to about 65 ha, whereas survival of natural nests decreases with increasing patch area. Effect sizes ( $\hat{\beta}$ ), standard errors (SE), 95% confidence intervals (CI), and relative importance measures (summed  $AIC_c$  weights;  $\Sigma w_i$ ) for the three explanatory variables (Patch area, Edge, and VegStruct) in the best model and across all models (model-averaged) for artificial and natural nests (Lark Bunting and Horned Lark). A positive  $\hat{\beta}$  indicates increased nest survival and a negative  $\hat{\beta}$  indicates decreased nest survival relative to a given predictor variable; a negative  $\hat{\beta}$  of the quadratic term indicates a curve that is concave downward. Data from Washington County, Colorado, summer 2000.

Variable	Artificial nests			Lark Bunting			Horned Lark		
	$\hat{\beta}$ (SE)	95% CI	$\Sigma w_i$	$\hat{\beta}$ (SE)	95% CI	$\Sigma w_i$	$\hat{\beta}$ (SE)	95% CI	$\Sigma w_i$
<b>Patch area</b>									
Best model	1.13 (0.47)	0.21, 2.03		-0.43 (0.21)	-0.85, -0.02		-0.38 (0.24)	-0.86, 0.09	
Model-averaged	1.05 (0.56)	-0.04, 2.14	0.876	-0.34 (0.26)	-0.84, 0.17	0.775	-0.21 (0.26)	-0.71, 0.30	0.546
<b>Patch area<sup>2</sup></b>									
Best model	-0.12 (0.06)	-0.23, -0.01		—			—		
Model-averaged	-0.12 (0.07)	-0.24, 0.01	0.876	—			—		
<b>Edge</b>									
Best model	-0.03 (0.07)	-0.16, 0.10		-0.02 (0.10)	-0.22, 0.17		-0.04 (0.12)	-0.27, 0.19	
Model-averaged			0.314			0.272			0.284
<b>VegStruct</b>									
Best model	-0.55 (0.37)	-1.28, 0.18		—			—		
Model-averaged	-0.30 (0.39)	-1.06, 0.45	0.532	-0.06 (0.28)	-0.61, 0.48	0.275	-0.05 (0.36)	-0.76, 0.65	0.279

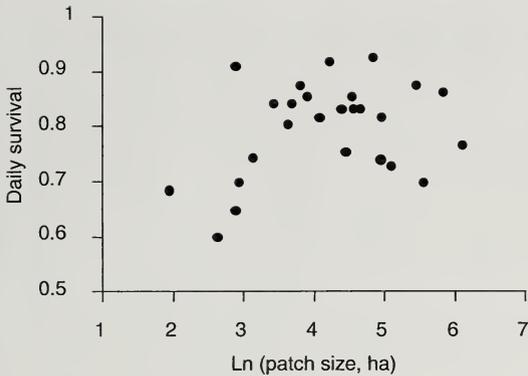


FIG. 1. Daily survival of artificial nests increased relative to  $\ln(\text{patch size})$  across 26 grassland patches in Washington County, Colorado, 2000. Artificial nest survival increased with patch area up to about 65 ha ( $\ln 65$  is approximately 4.2).

Artificial nest survival increased with patch area up to about 65 ha and differed little at larger patch sizes (Fig. 1; note that  $\ln 65$  is approximately 4.2). The strength of the relationship between patch area and daily nest survival is indicated by whether the 95% CI overlaps zero (Table 2). The 95% CI around the effect estimate for patch area<sup>2</sup> did not include 0 for the best model and slightly overlapped zero for the model-averaged estimate (that incorporates model-selection uncertainty). Nest survival increased as overall vegetation structure (VegStruc, a function of cover, height, and density) decreased, as indicated by the negative coefficients for the explanatory variable in the model-averaged estimate (Table 2); this relationship, however, is weak, as indicated by the extent of overlap of the 95% CI with zero.

*Nest success of Lark Buntings and Horned Larks.*—We found 36 Lark Bunting nests in 15 sites and 46 Horned Lark nests in 16 sites. Mean clutch size was  $4.4 \pm 0.17$  ( $n = 22$ ) and  $3.4 \pm 0.12$  ( $n = 33$ ) and number of young fledged per successful nest was  $2.9 \pm 0.26$  ( $n = 15$ ) and  $2.8 \pm 0.25$  ( $n = 13$ ) for Lark Buntings and Horned Larks, respectively. Daily survival rates of Lark Bunting and Horned Lark nests across all sites were  $0.891 \pm 0.022$  (95% CI = 0.847–0.935) and  $0.900 \pm 0.017$  (95% CI = 0.867–0.933). Overall nest survival was low, with only 10% of Lark Bunting nests and 11% of Horned Lark nests fledging at least one young. No nests were censored

from analyses due to suspected abandonment. Predator sightings in the grassland sites included ground squirrels, snakes, coyotes, striped skunks, and badgers.

The total area searched by rope-dragging during the season was 1,890 ha; 42% of this effort was within 50 m of site edges. Only 12 Lark Bunting and 6 Horned Lark nests were found within 50 m of the edge, which were fewer than expected if we assumed nest distribution to be random or uniform relative to habitat edges ( $\chi^2 = 5.6$ ,  $df = 1$ ,  $P < 0.010$ , and  $\chi^2 = 14.58$ ,  $df = 1$ ,  $P < 0.001$  for Lark Buntings and Horned Larks, respectively).

We chose patch area to represent area in the candidate models for Lark Buntings and Horned Larks because the quadratic form did not improve model performance (AIC<sub>c</sub> values differed by only 0.65 and 0.04 for Lark Buntings and Horned Larks, respectively) and the use of patch area offered greater parsimony. Daily survival of both Lark Bunting and Horned Lark nests was best explained by patch area alone (Table 1). For both species, nest survival decreased with increasing patch area, as indicated by the negative coefficients ( $\hat{\beta}$ ) for the explanatory variable in best models and model-averaged estimates (Table 2). For Lark Buntings, the 95% CI on the effect estimate for patch area did not include 0 (CI =  $-0.85$ ,  $-0.02$ ) in the best model but did slightly overlap zero with its model-averaged estimate (Table 2). In contrast, the 95% CI for Horned Larks barely overlapped zero in the best model and overlapped zero more so with the model-averaged estimate. The relative importance of patch area in influencing natural nest survival was stronger for Lark Buntings ( $\sum w_i = 0.775$ ) than for Horned Larks ( $\sum w_i = 0.546$ ). Edge and VegStruc had substantially smaller summed weights.

An alternative approach to examining patch-size effects on natural nest survival for this data set is to compute standard Mayfield (1975) estimates for grassland patches grouped as small (<80 ha) and large (>80 ha). Although not within the information-theoretic paradigm, the results of this analysis yielded similar results (Table 3). Nest survival was greater in small than in large patches for both species, with a somewhat stronger effect for Lark Buntings than for Horned Larks.

TABLE 3. Daily survival rates (SE, 95% CI) for Lark Bunting and Horned Lark nests were greater in small (<80 ha) than in large (>80 ha) grassland patches in Washington County, Colorado, summer 2000.

Grassland patch size	Lark Bunting			Horned Lark		
	<i>n</i>	Daily survival rate (SE)	95% CI	<i>n</i>	Daily survival rate (SE)	95% CI
Small (<80 ha)	15	0.925 (0.026)	0.874–0.975	25	0.912 (0.020)	0.873–0.952
Large (>80 ha)	21	0.851 (0.038)	0.776–0.925	21	0.881 (0.029)	0.824–0.937
	$t_{35} = 6.94, P < 0.001$			$t_{45} = 4.19, P < 0.001$		

## DISCUSSION

*Effects of prairie fragmentation on nest survival.*—In this study, survival of artificial nests increased with increasing patch size. This finding is consistent with general expectations of the effects of patch size on nest survival and with findings of grassland studies that incorporated patch sizes below 31 ha (Johnson and Temple 1990, Burger et al. 1994, Clawson and Rotella 1998, Winter et al. 2000). Grassland studies with minimum patch sizes exceeding 50 ha, however, found no effect of patch size on predation rates of artificial nests (Pasitschniak-Arts et al. 1998, Howard et al. 2001).

Our finding of a positive relationship between artificial nest survival and patch size, however, is the opposite of our findings on the survival of natural nests. Nests of Lark Buntings and Horned Larks had lower survival in the more extensive grassland patches in our study area. Ours is not the only study to document this unexpected trend. Higher daily survival was experienced by Baird's Sparrows (*Ammodramus bairdii*) in smaller patches of mixed-grass prairie (S. K. Davis pers. comm.), by several species of forest birds in forest fragments in western United States (Cavitt and Martin 2002), and by American Redstarts (*Setophaga ruticilla*) breeding in small, isolated stands of quaking aspen (*Populus tremuloides*; S. J. Hannon pers. comm.).

*Understanding the effects of fragmentation on predator communities.*—Predator communities exert a strong influence on avian fecundity. Numerous authors recently have suggested that effects of fragmentation on avian fecundity are highly complex and depend on predator dynamics within local landscapes, varying predator responses to fragmentation, and extent of fragmentation (e.g., Tewksbury et al. 1998, Heske et al. 2001, Patten and Bolger 2003). In general, the response of nest

predators to fragmentation is complex, taxon-specific, and landscape context-dependent (Chalfoun et al. 2002). Further, there are even within-species differences in responses to fragmentation and land conversion; for example, swift foxes in eastern Colorado and Wyoming tend to avoid agricultural lands (Finley 1999), whereas they do not do so in Kansas (Sovada et al. 2001b).

Once it is clearly acknowledged that predator communities differ across locales and regions, and that predator species differ in their hunting strategies and responses to habitat fragmentation (Chalfoun et al. 2002), there should be less expectation of clear and consistent relationships between fragmentation metrics and fecundity. Rather than simply asking what are the effects of fragmentation (degree of fragmentation, type of matrix, patch size, distance from edge) on avian fecundity, perhaps the pertinent questions should include: (1) what are the effects of fragmentation on predator communities, and (2) how do the resulting predator communities influence avian fecundity?

We hypothesize that our unexpected findings (of lower survival of natural nests with increasing patch area and different trends between artificial and natural nests) are due to differing composition of predator communities relative to patch sizes. Although we did not quantify predator populations, we did find patterns in artificial nest destruction relative to patch size that suggest that predator composition differs with patch size. The proportion of disturbed nests with broken quail eggs (rather than missing quail eggs or disturbed clay eggs) increased with increasing patch size ( $F_{1,23} = 6.340, P = 0.019$ ). It is likely that one (or just a few) predator species are responsible for the broken eggs, assuming that egg handling varies between predator species and is consistent within species.

Additional information to support that predator community composition differs with patch size is the variation in home-range sizes and area-sensitivity of local predators. The small grassland patches may be devoid of the larger mammalian predators because small patches provide insufficient habitat not compensated for by use of the matrix (agricultural fields). That mammalian predators are absent or in lower densities in the matrix habitat than in the grassland habitats is suggested by lower predation rates on Mountain Plover (*Charadrius montanus*) nests in agricultural fields than in native prairie (F. L. Knopf and V. J. Dreitz pers. comm.), by small mammal movements out of barren cropland (Streubel and Fitzgerald 1978, Cummings and Vessey 1994), and by lower security of den sites in tilled agricultural lands.

All of our grassland patches, even the smallest 7-ha patch, contained thirteen-lined ground squirrels (average home range = 1–5 ha; Streubel and Fitzgerald 1978) and snakes. We suspect that only the larger patches are frequented by the larger mammalian carnivores, such as badgers (mean home range = 725 ha; Long 1973), striped skunks (mean home range = 378–512 ha; Wade-Smith and Verts 1982), coyotes (mean home range = 19.8 km<sup>2</sup>; Kitchen et al. 1999), and possibly swift foxes (mean home range = 7.6 km<sup>2</sup>; Kitchen et al. 1999). Additionally, densities of thirteen-lined ground squirrels may be greater in the smaller fragments; if larger predators are absent, numerical increases of ground squirrels may occur in a process similar to “mesopredator release” (Crooks and Soule 1999, Heske et al. 2001). This reasoning is consistent with Vander Haegen et al. (2002), who report that the composition of predator communities differs between fragments and contiguous tracts of shrubsteppe habitat.

Our study and other recent studies have demonstrated that trends in mortality of artificial nests do not always mimic trends of natural nests (Valkama et al. 1999, Zanette 2002, Mezquida and Marone 2003). These discrepancies may be due to differences in predator communities between treatments and the ways in which individual predators respond to artificial and natural nests. Eggs in artificial nests cannot be camouflaged by incubating adults or protected by the defensive actions of

parents. In natural nest trials, on the other hand, parental presence can either attract or deter nest predators. Adult Lark Buntings, and probably Horned Larks, can deter ground squirrel nest predation; several Lark Buntings have been filmed chasing ground squirrels from their nests (J. B. Barna and A. S. Chaine pers. comm., but see Pietz and Granfors 1994). We also commonly witnessed adults of both species chasing ground squirrels. Parental behavior and scent may attract the larger mammalian predators, but nest defense probably cannot deter them. The idea that small grassland patches have greater densities of small predators or ground squirrels, which search for nests randomly, is consistent with our finding of lower survival of artificial nests in smaller patches. Likewise, the idea that larger patches have more predators that use cues of adults to find nests rather than random search is consistent with our finding of lower survival of natural nests in larger patches.

*Implications for management.*—For management to be effective in reversing population declines in grassland birds, the ultimate factors underlying the declines must be identified and addressed. Even if it is determined that low reproductive success due to predation in breeding areas is a primary driver of population declines, the available management tools are not extensive. Predator control as a means of improving reproductive success of songbirds is generally not advocated because removal of one subset of predators at a local site is compensated for by numerical increases or changes in foraging habits of another subset (Reitsma et al. 1990; Dion et al. 1999, 2000; Heske et al. 2001). Manipulations of habitat features at a local scale, although labor-intensive and costly, have met with some success in improving avian reproductive output (Morse and Robinson 1999, Heske et al. 2001, Sovada et al. 2001a).

Current recommendations for acquisition, restoration, and management of forest and grassland habitats are often based on patch size (Robinson et al. 1995, Heske et al. 2001), and landscape manipulations often include the protection and consolidation of large habitat tracts. This approach is justified by the many studies with positive relationships between forest area and bird abundance and/or nest survival and is especially applicable to land-

scapes with considerable native habitat remaining. We question, however, as do others (Friesen et al. 1999, Bakker et al. 2002, Cavitt and Martin 2002, Patten and Bolger 2003), whether the effects of habitat fragmentation can be generalized across regions, landscapes, and habitats—and whether the protection of only large habitat tracts is the best approach in all areas. The value of small habitat patches in agricultural landscapes is often overlooked (Friesen et al. 1999); even small patches can function as population sources in some years (S. J. Hannon pers. comm.). We do not question the value of extensive grasslands nor justify further fragmentation of native grassland, but we do encourage additional incentive programs for habitat conservation of small patches, when appropriate, in fragmented agricultural landscapes.

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## COMPARISON OF DAILY AVIAN MORTALITY CHARACTERISTICS AT TWO TELEVISION TOWERS IN WESTERN NEW YORK, 1970–1999

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**ABSTRACT.**—Recent increases in the demand for communication towers have renewed interest in the impact of these towers on birds, particularly during migration. The objective of this study was to investigate avian mortality at two television towers (WGRZ and WKBW) in western New York from 1970 through 1999. Daily mortality totals ranged from 1 to 1,089 birds. The majority of the kill events were small, involving 10 or fewer birds; however, the majority of birds died in larger kill events. Both kill events and the numbers of individuals salvaged peaked in September. Patterns in avian mortality at the towers that we studied were consistent with normal migration events, during which the number of birds migrating varies substantially between nights. The two towers differed significantly in kill characteristics. At the WGRZ tower, median daily mortality generally ranged from 1 to 10 birds and was usually lower than at the WKBW tower. The size of kill events varied across the 3 decades, with no very large kill events (>500 birds) occurring in the 1990s. Because most birds salvaged in the 1970s and 1980s were killed in medium and large kill events, the absence of any very large kill events in the 1990s could explain the previously published decline in birds salvaged at these towers. *Received 24 May 2004, accepted 7 February 2005.*

Although the Migratory Bird Treaty Act of 1918 prohibits human interference with migratory birds, lighted man-made structures, such as communication towers, have been responsible for the deaths of many nocturnal migrants (Avery et al. 1980). Avian mortality at communication towers (tower kill) results from collisions of birds with the towers themselves or their supporting guy cables. In the United States, there are more than 83,000 towers (Federal Communications Commission 2004), and the number of tower kills is likely to increase as tower construction continues. Many factors affect the number of nocturnal migrants colliding with towers, including density of migrants aloft, weather, tower location and elevation, tower height, number and location of guy cables, and lighting. Northerly winds spur bird migration in the fall, and overcast conditions may disorient birds, resulting in their gravitation toward lighted towers (Clark 1973).

Only a few long-term studies have documented the effects of specific towers on avian mortality. Crawford and Engstrom (2001) noted that the pattern of avian mortality they wit-

nessed at a northern Florida television tower was “distinctly seasonal,” with most of the kill events occurring during fall migration. In a study of tower mortality in western New York and Ohio, Morris et al. (2003) documented a significant decline in the number of salvaged birds over a 30-year period. This decrease could result from fewer kill events, smaller kill events, or both.

The goal of our study was to examine patterns of avian mortality at two television towers in western New York. Specifically, we documented temporal patterns in the kill events, both within the autumnal migratory period and among the last 3 decades.

### METHODS

We examined fall avian mortality at two television towers in southern Erie County during the 30-year period from 1970 to 1999. The WGRZ tower is located in Wales, New York (78° 33' N, 42° 43' W); it is 261 m tall, not including a 32-m antenna, and was erected in 1968. This tower sits at an elevation of 412 m asl and is supported by 15 guy cables. Additionally, it is illuminated at night by three levels of constantly burning, red obstruction-warning lights (three lights per level, 116 watts each) and three levels of slowly flashing, red beacon lights (1,240 or 1,400 watts each). The WKBW tower is located in Colden, New York (78° 37' N, 42° 38' W); it is

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TABLE 1. Annual variation in daily avian kill events at two television towers in western New York during fall migration, 1970–1999.

Year	WGRZ					WKBW				
	Number of visits	Number of kill events	Median <sup>a</sup>	Range	Total no. of birds killed	Number of visits	Number of kill events	Median <sup>a</sup>	Range	Total no. of birds killed
1970	NA <sup>b</sup>	18	14.5	1–630	1,828	NA <sup>b</sup>	12	14.5	1–90	240
1971	67	23	11	1–361	852	67	28	5	1–72	434
1972	NA <sup>b</sup>	9	5	1–98	174	NA <sup>b</sup>	2	4.5	2–7	9
1973	NA <sup>b</sup>	11	5	1–88	158	NA <sup>b</sup>	8	7	1–17	69
1974	NA <sup>b</sup>	15	9	1–51	237	NA <sup>b</sup>	8	27.5	1–307	829
1975	NA <sup>b</sup>	9	38	3–458	1,066	NA <sup>b</sup>	8	64	3–686	1,312
1976	17	14	8.5	1–110	304	12	8	13.5	2–55	170
1977	15	10	7.5	1–170	391	13	11	5	1–445	1,026
1978	27	12	10	1–70	209	13	8	4	1–114	171
1979	25	14	6	1–63	179	15	15	9	1–138	345
1980	29	13	9	1–135	331	15	9	4	1–659	984
1981	13	5	5	1–100	116	6	4	12.5	1–91	117
1982	24	19	13	1–437	1,189	18	15	35.5	1–1,089	3,306
1983	21	7	2	1–76	97	11	3	11	3–23	37
1984	16	12	3	1–42	116	9	5	22	1–98	178
1985	20	9	4	1–68	173	8	4	45.5	1–159	251
1986	17	6	4	1–40	63	7	3	11	6–113	130
1987	12	1	1	1	1	5	4	1.5	1–42	46
1988	10	4	7	3–98	115	7	4	17.5	1–262	298
1989	12	3	1	1–72	74	5	3	58	2–332	392
1990	16	9	4	1–43	83	8	5	22	2–65	140
1991	13	5	1	1–8	19	4	2	5	1–9	10
1992	10	4	1	1–2	5	2	1	1	1	1
1993	8	6	3	1–60	75	4	3	6	3–15	24
1994	12	6	1	1–15	23	3	2	37.5	12–63	75
1995	10	7	2	1–10	20	4	3	2	1–3	6
1996	12	8	3	1–13	36	9	5	28	2–294	426
1997	12	7	1	1–10	26	5	3	3	1–9	13
1998	15	8	1	1–3	12	5	2	1	1	2
1999	23	11	3	1–13	45	13	7	5	1–23	51
Total	518	285	4 <sup>c</sup>		8,017	306	195	6 <sup>c</sup>		11,092

<sup>a</sup> Median number of birds collected after nights with kill events (nights with no birds were excluded).

<sup>b</sup> The number of days visited without finding birds was not recorded in the early 1970s.

<sup>c</sup> Overall median was based on all kill events, not on annual medians.

305 m tall, not including a 23-m antenna, and was erected in 1958. This tower sits at an elevation of 529 m asl and is supported by 18 guy cables. The WKBW tower has four levels of red obstruction-warning lights and four levels with red beacon lights and is located approximately 8 km south-southwest of the WGRZ tower. Both towers are a lattice of steel, and triangular in cross-section, typical of many television and radio towers. Both tower sites have paved driveways, small parking lots, and transmitter buildings. Immediately surrounding the facilities are grass lawns cut lower than surrounding grass. At WKBW, the taller grass fields were cut in early fall during most years of the study. At WGRZ,

there were larger areas of cut grass and pavement to the south of the tower. The taller grass fields were used as pasture in the early years of the study, with occasional cuttings in the later years.

With the assistance of volunteers, ARC salvaged birds from the WGRZ and WKBW towers. Visits to towers generally occurred from late August to early November, following nights with overcast or mostly overcast skies and with northerly winds or winds becoming northerly. Although records were kept of most visits during which no salvaged birds were recovered, this information was more thoroughly documented after 1975 (Table 1). The search procedure involved checking the

TABLE 2. Top five families of birds killed at two television towers in western New York, 1970–1999. Most of the birds salvaged at both towers were members of Parulidae, Turdidae, Vireonidae, and Regulidae.

Total birds killed at each tower by family	
WGRZ	WKBW
5,055 Parulidae	7,410 Parulidae
1,030 Turdidae	1,694 Turdidae
689 Vireonidae	1,086 Vireonidae
624 Regulidae	346 Regulidae
337 Emberizidae	207 Mimidae

paved and grassy areas around the towers for birds by walking in loops (ranging out to approximately 50 m at WGRZ and 60 m at WKBW) through the lower-cut grass lawns and by walking straight lines under the guy cables to about 65 m from the base of the tower, and by returning about 2 m south of the cables. The searches included additional loops out into taller grass to approximately 30 m from the tower in the two southerly facing angles of the guy cables.

Searchers increased coverage of grassy areas when specimens were found, walking a series of parallel paths approximately 1 m apart on the lower-cut grass lawns. Searchers walked similar patterns in the taller grass, extending well beyond the last specimen collected. Using binoculars, searchers also checked the angled roof of the WGRZ transmitter building for birds (Morris et al. 2003).

To compare avian mortality across decades, we designated kill sizes as small (1–10 birds),

medium (11–100 birds), and large (>100 birds). We used likelihood ratio chi-square tests to analyze differences in kill sizes between towers and among decades at each tower, and differences in the number of individuals in kill events among the 3 decades. We examined temporal patterns during fall migration by 10-day periods beginning 1 August. We salvaged birds between 12 August and 16 November, resulting in 10 pooling intervals. Because of limited collections in August and November, we combined the first two periods into a single initial interval, and the last two periods into a single final interval, resulting in eight intervals for statistical analysis. We pooled data across each decade to investigate temporal changes during the 30-year period. We present median kill sizes because distributions were not normal. All analyses were performed using SYSTAT (SPSS, Inc. 2002). Significance levels were determined after sequential Bonferroni correction for multiple tests (Rice 1989), although uncorrected *P*-values are presented.

## RESULTS

From 1970 through 1999, 11,092 birds were collected at the WKBW-TV tower, and 8,017 birds were collected at the WGRZ-TV tower. At least one bird was salvaged most nights (WGRZ: 55.0%,  $n = 518$ ; WKBW: 63.7%,  $n = 306$ ), although nights on which no birds were collected were not always noted, particularly in the early 1970s (Table 1). The families represented most frequently were similar at the two towers (Table 2). The top

TABLE 3. The most commonly killed avian species were similar at two television towers in western New York, 1970–1999.

Species	Total killed at WGRZ	Species	Total killed at WKBW
Ovenbird ( <i>Seiurus aurocapilla</i> )	907	Bay-breasted Warbler	1,359
Magnolia Warbler ( <i>Dendroica magnolia</i> )	555	Ovenbird	1,303
Swainson's Thrush ( <i>Catharus ustulatus</i> )	531	Magnolia Warbler	986
Bay-breasted Warbler ( <i>Dendroica castanea</i> )	494	Swainson's Thrush	865
Blackpoll Warbler ( <i>Dendroica striata</i> )	487	Red-eyed Vireo	806
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	472	Black-throated Blue Warbler	437
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	444	Blackpoll Warbler	405
Black-throated Blue Warbler ( <i>Dendroica caerulescens</i> )	348	Tennessee Warbler ( <i>Vermivora peregrina</i> )	391
American Restart ( <i>Setophaga ruticilla</i> )	239	Common Yellowthroat ( <i>Geothlypis trichas</i> )	366
Black-throated Green Warbler ( <i>Dendroica virens</i> )	227	Black-throated Green Warbler	325

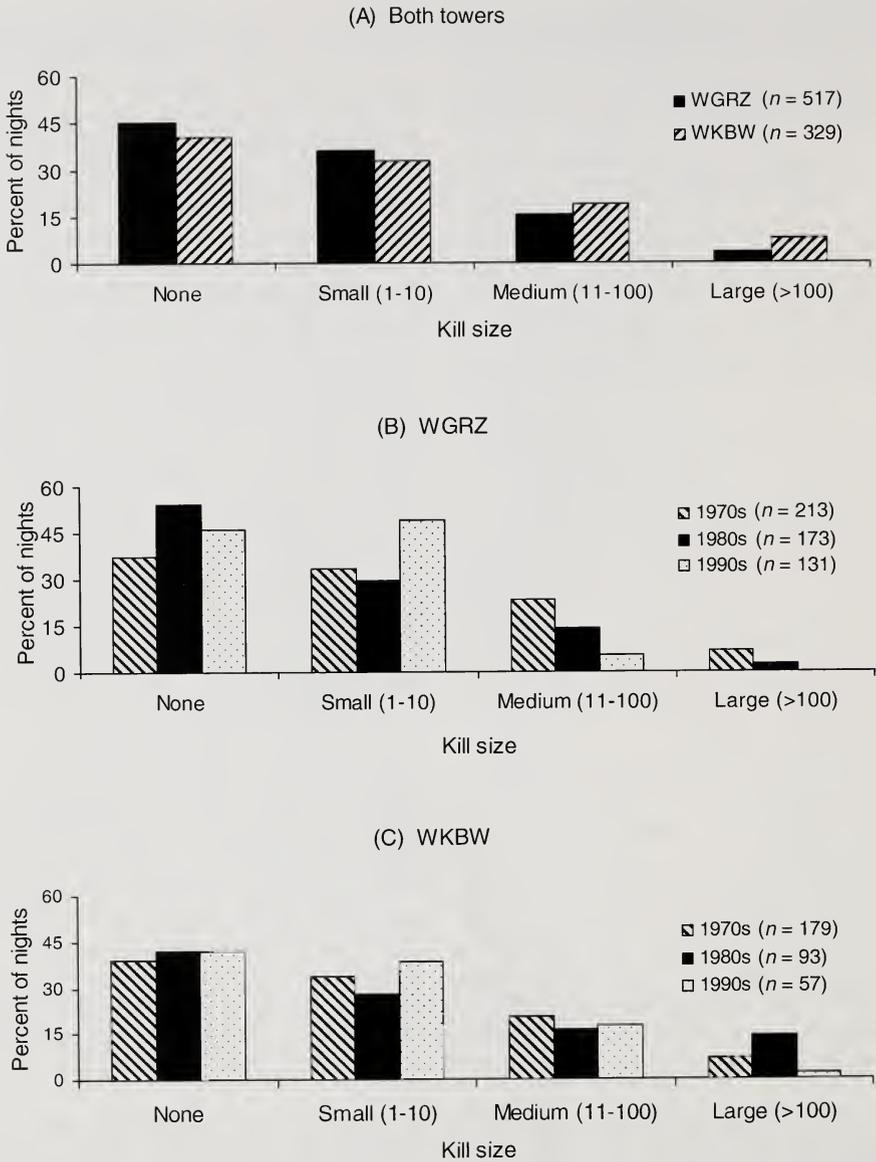


FIG. 1. Kill events at two television towers in western New York, 1970–1999: (A) totals for each tower; (B and C) totals by decade for the WGRZ and WKBW towers. The majority of collections resulted in 100 or fewer birds killed during a single night.

ten species killed at each tower represented >50% of the total individual birds killed, and all but one of these species were Neotropical migrants (Table 3).

The number of birds killed per night ranged from 1 to 1,089 at WKBW and from 1 to 630 at WGRZ. Kill events on most nights involved 10 or fewer birds (Fig. 1). The median kill

size (all years) was four at WGRZ and six at WKBW (Table 1). We detected a slight but significant difference in the proportion of small, medium, and large kill events between the two towers ( $\chi^2 = 8.5$ ,  $df = 2$ ,  $P = 0.014$ ; Fig. 1A). The proportion of small, medium, and large kill events was dependent on decade (WGRZ:  $\chi^2 = 30.6$ ,  $df = 4$ ,  $P < 0.001$ ;

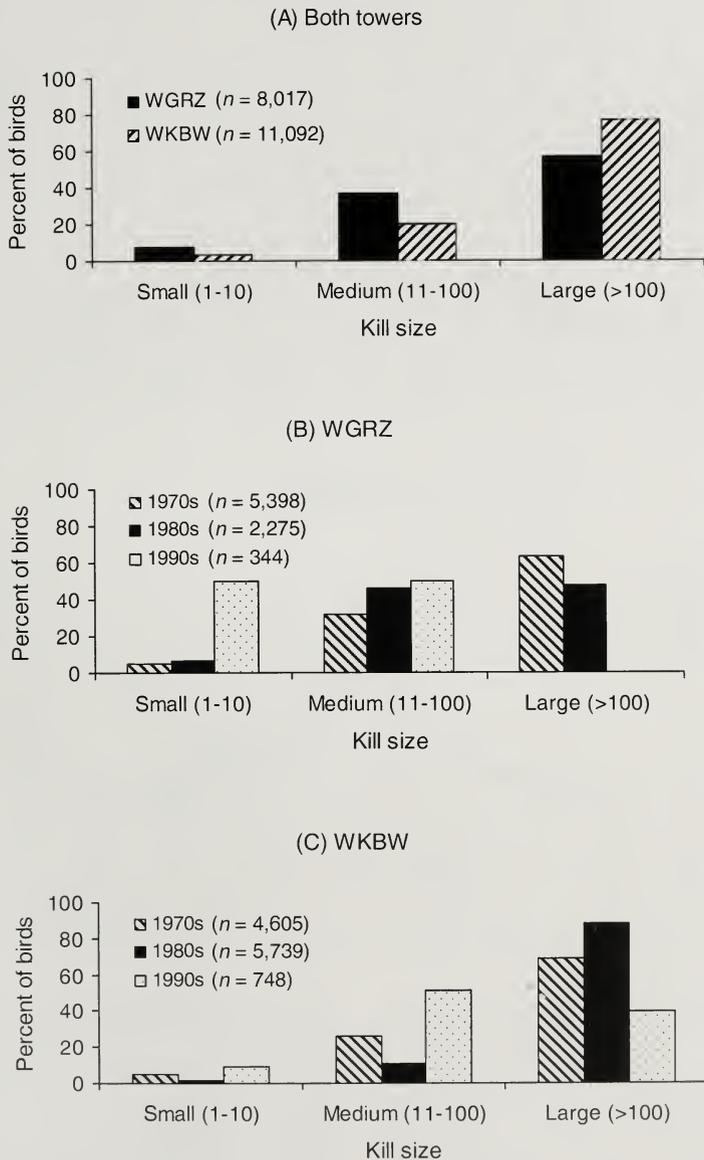


FIG. 2. Birds salvaged at two television towers in western New York, 1970–1999: (A) percent salvaged at each tower; (B and C) percent salvaged by decade for the WGRZ and WKBW towers. A relatively small percentage of salvaged birds was collected after nights when kill sizes were small (10 or fewer).

WKBW:  $\chi^2 = 10.0$ ,  $df = 4$ ,  $P = 0.040$ ), with a higher proportion of small kill events in the 1990s at both towers (Fig. 1B, C).

Although most kill events involved 10 or fewer birds, the majority of birds were salvaged after medium to large kill events (>10 birds; Fig. 2). The majority of individuals were killed in large events during the 1970s and 1980s at both towers, while the majority of individuals were killed in small and medi-

um events in the 1990s (WGRZ:  $\chi^2 = 987.7$ ,  $df = 4$ ,  $P < 0.001$ ; WKBW:  $\chi^2 = 1,101.5$ ,  $df = 4$ ,  $P < 0.001$ ; Fig. 2B, C). During the 1990s, there were substantially fewer birds collected overall, and no single kill event resulted in a very large kill (>500 individuals). The largest kill event during that decade at WGRZ was only 60 birds; only one kill event was >100 birds at WKBW (294 birds on 10 September 1996).

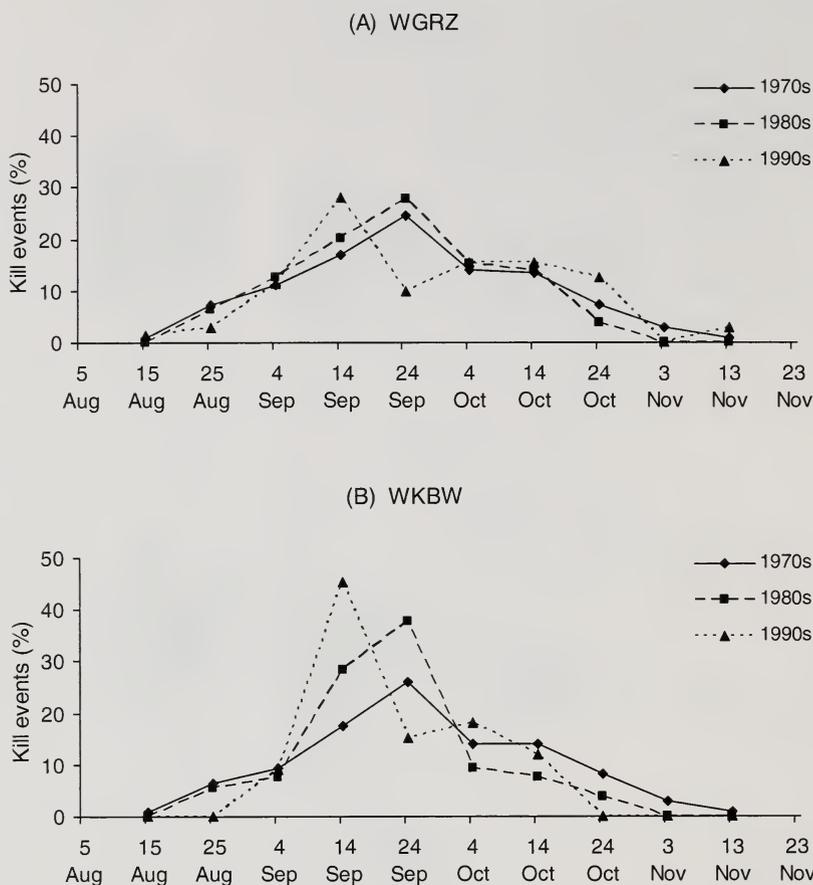


FIG. 3. Kill events (%) by 10-day salvage intervals at two television towers in western New York, 1970–1999. At both towers, the largest percentage of nights during which birds were killed occurred during September.

Kill events occurred throughout autumn migration, with most occurring during September (Fig. 3). The proportion of kill events by 10-day salvage interval did not differ among the 3 decades (WGRZ:  $\chi^2 = 20.1$ ,  $df = 14$ ,  $P = 0.126$ ; WKBW:  $\chi^2 = 25.9$ ,  $df = 14$ ,  $P = 0.027$ ; not significant after Bonferroni correction). Similar to the timing of kill events, the largest proportion of migrants was salvaged in September (Fig. 4). In the 1970s and 1980s, the largest kill events occurred in mid-September, while in the 1990s, the largest kill events occurred in early September. This pattern was observed at both WGRZ and WKBW; additionally, the proportion of salvaged birds by 10-day interval differed among the 3 decades (WGRZ:  $\chi^2 = 926.2$ ,  $df = 14$ ,  $P < 0.001$ ; WKBW:  $\chi^2 = 2,583.8$ ,  $df = 14$ ,  $P < 0.001$ ). These analyses are dependent on the timing of visits to the tower sites; thus, we

investigated whether the timing of visits varied across the 3 decades. We found no difference in the proportion of visits to towers by 10-day salvage interval for both towers (WGRZ: likelihood ratio  $\chi^2 = 17.7$ ,  $df = 14$ ,  $P = 0.22$ ; WKBW: likelihood ratio  $\chi^2 = 24.6$ ,  $df = 14$ ,  $P = 0.039$ ; not significant after Bonferroni correction). The slight difference in the timing of visits at WKBW across the 3 decades was due to the highest percentage of visits occurring in mid-September in the 1990s (30.4% of all visits) versus late September in the 1970s (19.3%) and 1980s (27.0%).

## DISCUSSION

Avian mortality at towers may reflect not only the abundance of migrants, but also the weather conditions migrants experience. Furthermore, individual communication towers appear to differ in their impact on migrants.

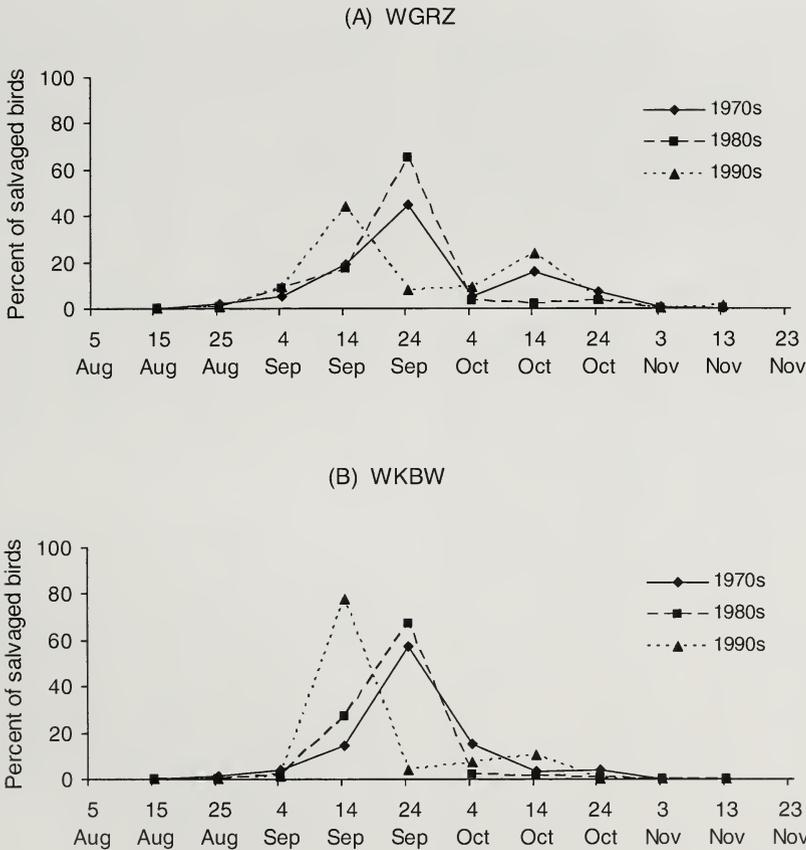


FIG. 4. Salvaged birds (%) by 10-day intervals at two television towers in western New York, 1970–1999. Most birds were collected during September.

Thus, finding dead birds at either tower in this study most likely indicated migration was occurring. However, even nights with appropriate wind conditions for migration (northerly) did not always result in substantial avian mortality. Most visits to both television towers resulted in the salvage of migrants. Although most visits resulted in the salvage of 10 or fewer birds, on some we recorded large kill events (>100 birds). These results are similar to those from a study in northern Florida, in which small kill events occurred on more than 80% of days (Crawford and Engstrom 2001). Likewise, Crawford and Engstrom (2001) reported a very low percentage of very large kill events (0.1% of days resulted in the salvage of >500 individuals); the combination of appropriate wind conditions and cloud cover were necessary for substantial kill events (Clark 1973, Crawford and Engstrom 2001). Nights with no birds salvaged were frequent

in this study and may reflect a lack of migration or weather conditions that were not conducive to tower kills.

Crawford and Engstrom (2001) noted that more than 40% of birds were salvaged from kill events of 11–100 birds. Furthermore, although only one bird was salvaged after >30% of nights, only approximately 2% of all individuals were salvaged after those nights. Our results are similar in that only a very small percentage of birds were from salvages of single individuals, and most of the birds we salvaged were collected after medium (11–100 birds) or large (>100 birds) kill events.

We did find slight but significant differences in the sizes of kill events between the two towers studied. Detailed comparisons of avian mortality can be hampered by a number of variables whose effects may be difficult or impossible to isolate. The two towers in this study, although structurally similar, differ in

elevation at ground level, tower and antenna height above ground, number and placement of guy cables, building and grounds lighting, surrounding habitat, and proximity to other towers (Clark 1973, Morris et al. 2003). The WKBW tower had a higher proportion of large kill events than the WGRZ tower, was taller and located at a higher elevation, and had more guy cables.

Previous work has documented that significantly more birds were killed at these television towers in the 1970s and 1980s than in the 1990s (Morris et al. 2003). Thus, it is not surprising that the majority of individuals were salvaged from large kill events (>100 individuals) during the 1970s and 1980s. The decrease in the number of birds salvaged during the 1990s reflects the smaller kill events documented in the results presented here. Reasons for the decline in the number of birds salvaged remain unknown, although the declines may reflect a decline in migrant populations (Goodpasture 1984), a change in weather patterns (Goodpasture 1984), selection against lower-flying migrants, an increase in anthropogenic nocturnal lighting (Morris et al. 2003), and/or an increase in predation on the avian casualties at towers (Stoddard 1962, Goodpasture 1984, Crawford and Engstrom 2001).

Peak kill events at both towers occurred in mid-September during the 1970s and 1980s, whereas during the 1990s, kill events peaked in early September. Likewise, the majority of individual birds were salvaged in mid-September for both towers in the 1970s and 1980s, while in the 1990s the peak occurred in early September. Fall migration in western New York generally shows a peak in September, particularly among Neotropical migrants (Buffalo Ornithological Society 2002). Because there were few large kill events in the 1990s (and, therefore, our salvage data for the 1990s are based only on small and medium kill events), our results may not reflect any real change in migration timing across decades.

Although most tower kill events, particularly in recent years, have been small at individual communication towers, the cumulative impact of small kill events at thousands of towers may greatly impact migrant populations. Migration is an extremely hazardous

period for birds. Among Black-throated Blue Warblers (*Dendroica caerulescens*), for example, approximately 85% of annual mortality may occur during this period (Sillert and Holmes 2002). Many causes may contribute to mortality during migration, but clearly collisions with communication towers have an impact on migrant populations. It is speculated that millions of birds are killed at communication towers annually, and this threat is expected to double in the next decade as the proliferation of communication towers continues (Holden 2001). The relative impact of collisions with towers and other causes of mortality during migration require additional study.

#### ACKNOWLEDGMENTS

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## A NEW MODEL TO ESTIMATE DAILY ENERGY EXPENDITURE FOR WINTERING WATERFOWL

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**ABSTRACT.**—Current models to estimate daily energy expenditure (DEE) for free-living birds are limited to either those that use fixed thermoregulatory costs or those that more accurately estimate thermoregulatory costs, but require extensive and often logistically difficult measurements. Here, we propose a model based on basal metabolic rate (BMR), activity budgets, and site-specific energetic costs of thermoregulation that requires only simple measures of ambient temperature and wind speed to provide estimates of DEE. We use the model to calculate the DEE of Buffleheads (*Bucephala albeola*) wintering at six habitats that afford differing degrees of protection from exposure within Narragansett Bay, Rhode Island. Bufflehead activity budget data collected during the winters of 2001–2002 and 2002–2003, along with average temperatures and wind speeds at the sites, were used to calculate DEE that ranged from 46.9 to 52.4 kJ/hr and increased with increasing wind speed. The energetic cost of thermoregulation composed as much as 28% of total DEE and increased with wind speed. Our DEE values were 13.4% higher, and thermoregulatory costs were up to 2× higher than those calculated using an existing model that incorporates fixed thermoregulatory costs. We also saw an increase in feeding activity with increasing wind speed; sensitivity analysis of the effects of wind speed and feeding activity showed that a 1 m/sec increase in wind speed at our sites increased DEE by 2.5%, whereas a corresponding increase in feeding activity increased DEE by 4.5%. This suggests that in temperate winter habitats, increased feeding activity may have a greater impact on Bufflehead DEE than wind exposure. Site-specific model estimates of DEE could also provide additional insight into the relative contribution of environmental conditions and changes in waterfowl behavior to DEE. Received 27 May 2004, accepted 12 January 2005.

The daily energy expenditure (DEE) of a species is the sum of basal metabolic rate (BMR), thermoregulatory requirements, and the energetic cost of daily activities such as feeding, locomotion, and social behaviors. Quantitative assessments of the daily activities of wintering waterfowl have been used both to identify important habitats for these species and to assess their response to changes in habitat quality (Fredrickson and Drobney 1979, Brodsky and Weatherhead 1985a, Baldassarre et al. 1988, Paulus 1988). Waterfowl activity budgets may be influenced by habitat type (Turnbull and Baldassarre 1987, Rave and Baldassarre 1989) and site characteristics such as food abundance, protection from exposure, and level of disturbance (Nilsson 1970, Jorde et al. 1984, Paulus 1984, Quinlan and Baldassarre 1984, Brodsky and Weatherhead 1985b, Miller 1985). Changes in waterfowl activity may also be tied to changes in DEE that result

from the influence of habitat characteristics. For example, increased exposure to cold and wind may increase thermoregulatory energy costs, and therefore require increased feeding to offset higher energetic costs (Bennett and Bolen 1978, Hickey and Titman 1983). Models that allow comparison between the energetic costs of thermoregulation and specific waterfowl behaviors could be used to determine the relative magnitude of these costs, and may also provide insight into the effects of habitat quality on the DEE of resident waterfowl.

Traditional measures of DEE for birds from time-activity budgets use multiples of BMR to estimate energetic costs of activities, but may differ in how the thermoregulatory component of DEE is estimated (Weathers et al. 1984). Early estimates of DEE included either a fixed cost of thermoregulation or one based solely on ambient temperature (Kendeigh 1949, Schartz and Zimmerman 1971, Koplín et al. 1980). Models subsequently evolved to include a means to more accurately estimate thermoregulatory costs, but only by the extensive measurement of many variables (e.g., whole-body thermal resistance, forced-convective resistance), some of which may be logistically difficult to obtain for free-living

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wildlife (Pearson 1954, Stiles 1971, Walsberg 1977). Weathers et al. (1984) proposed the use of standard operative temperature, or indices that allow single-number representations of complex thermal environments, to overcome some of these difficulties. However, while providing a much more rigorous estimate of thermoregulatory costs, this approach is limited by the need for the construction and calibration of taxidermic mounts, and may be best suited for aviary or well-controlled field applications. To date, researchers estimating DEE for free-living birds using published activity-based models are limited to either those that use fixed thermoregulatory costs or those that more accurately estimate thermoregulatory costs, but at the expense of extensive and often logistically difficult measurements of many variables.

Previous studies estimating DEE for wintering waterfowl have employed models that use factorial increases of BMR and that assume a fixed cost of thermoregulation (Woolley and Owen 1978, Albright et al. 1983, Morton et al. 1989, Parker and Holm 1990). For wintering waterfowl in northern areas exposed to low temperatures and high winds, thermoregulation may compose as much as 80% of daily energetic costs (Ettinger and King 1980, Walsberg 1983). These costs may vary between wintering habitats because of differing degrees of protection from exposure to wind and cold (Porter and Gates 1969, Goldstein 1983, Bakken 1992). If estimates of DEE are to be useful in assessing habitat quality for wintering waterfowl, they need to include some measure of the energetic cost of thermoregulation based on local environmental conditions.

Here, we present an activity-based model that includes habitat-specific measures of thermoregulatory costs to estimate DEE of waterfowl in different habitats. Our model requires only simple measures of ambient temperature and wind speed, along with waterfowl activity budgets and morphological measurements. Thermoregulatory costs are calculated by using heat loss via conduction and convection as a function of temperature and wind speed to estimate the metabolic heat production required to maintain body temperature (Birkebak 1966, Goldstein 1983). Because of the ability to estimate site-specific DEE based on

local conditions, the model may be useful in evaluating habitats that provide differing degrees of protection from high winds and extreme temperatures. Model estimates could also be used to provide insight into the relative contribution of environmental conditions and differences in waterfowl behavior to changes in DEE.

In this study, we used our model to estimate the DEE of Buffleheads (*Bucephala albeola*) at six wintering habitats in Narragansett Bay, Rhode Island, that afford differing degrees of protection from exposure to wind and cold temperatures. Our specific objectives were to (1) compare estimates of DEE obtained using our model with those obtained using a previously published model that incorporates a fixed cost of thermoregulation, and (2) examine changes in DEE across the sites and determine the relative contribution of wind speed and waterfowl feeding behavior to changes in DEE.

## METHODS

*DEE site-specific thermoregulation model.*—Our model incorporating site-specific thermoregulatory costs into DEE for wintering Buffleheads (hereafter, SST model) consists of (1) a thermoregulatory component ( $EE_{\text{Thermoreg}}$ )—an estimate of the metabolic heat production required to balance heat loss from the bird to the environment through conduction and convection, and (2) an activity component ( $EE_{\text{Activity}}$ )—an estimate of additional energetic costs resulting from specific daily activities of wintering Bufflehead expressed as multiples of basal metabolic rate (BMR). We sum these components to arrive at an estimated DEE. In our model, metabolic heat production includes resting energy expenditure in a thermoneutral environment (i.e., BMR) and the additional energy expenditure required to maintain thermal equilibrium. The model uses average temperatures and wind speeds that coincide with activity budget sampling at the sites; DEE is reported in kJ/hr.

Basal metabolic rates were estimated from those of 16 North American duck species summarized in McNab (2003). A plot of BMR versus body mass for these species gave the relation:  $BMR = 4.05M^{0.79}$ , where BMR is basal metabolic rate in ml  $O_2$ /hr, and M is body mass in g. Estimates of BMR were con-

verted to kJ/hr using a conversion factor of 18.8 kJ/L O<sub>2</sub>, derived from the average composition of the Bufflehead's winter diet (Schmidt-Nielsen 1997). Body mass was approximated at 450 g for males and 325 g for females (Gauthier 1993).

Before calculating metabolic heat production, we first determined when this component of a Bufflehead's DEE is necessary by comparing ambient temperature with their lower critical temperature, or the temperature below which metabolic heat production is required to maintain body temperature (Schmidt-Nielsen 1997). Lower critical temperature (LCT) was estimated by the empirical relation:  $LCT = 47.2M^{-0.18}$ , where LCT is in °C, and M is body mass in g (Kendeigh 1977). We compared effective ambient temperature ( $T_{ef}$  or the ambient temperature corrected for the effect of wind speed; Siple and Passel 1945) to LCT to determine whether metabolic heat production would be required to maintain the duck's body temperature. If  $T_{ef}$  was less than LCT, we assumed that metabolic heat production was required to maintain body temperature; we then calculated this energy requirement and included it in the final DEE. On the other hand, if  $T_{ef}$  was greater than the lower critical temperature, we did not include metabolic heat production. Effective temperature was calculated using the relationship derived by Siple and Passel (1945):

$$T_{ef} = T_b - (T_b - T_a) \times (0.474 + 0.239 \times \sqrt{u} - 0.023 \times u),$$

where  $T_{ef}$  is the effective temperature (°C) used for comparison with the lower critical temperature,  $T_b$  is body temperature (°C),  $T_a$  is ambient temperature (°C), and  $u$  is wind speed (m/sec).

If  $T_{ef}$  was less than LCT, we used an empirical model to estimate metabolic heat production as a function of temperature and wind speed (Goldstein 1983):

$$H_{T+u} = a + b\sqrt{u},$$

where  $u$  is wind speed (m/sec) and  $H_{T+u}$  is metabolic heat production (watts). The coefficient  $b$  is determined empirically from data summarized by Goldstein (1983) on seven species of birds (body size 13.5–3,860 g) by the relation:  $b = 0.0092M^{0.66} \times \Delta T^{0.32}$ , where

$M$  is body weight in g and  $\Delta T$  is the difference between lower critical temperature and ambient temperature in °C. The coefficient  $a$  is determined under conditions of free convection ( $u = 0.06$  m/sec) by the relation:

$$a = H_T - b\sqrt{0.06},$$

where  $H_T$  is an adjusted metabolic rate in watts at ambient temperature (Goldstein 1983). We estimated  $H_T$  using a heat transfer model proposed by Birkebak (1966) that calculates conductive heat loss from different anatomical regions of the bird to the environment using geometrical representations (e.g., head represented as a sphere, body represented as a cylinder) and heat transfer theory (Appendix; Birkebak 1966). Morphological measures of body dimensions (Fig. 1) can be obtained from the literature (e.g., Belrose 1980, Gauthier 1993) or from measurements of museum specimens. Average values for live Buffleheads ( $n = 4$ , obtained from the Connecticut Waterfowl Trust, Farmington, Connecticut) and Bufflehead study skins ( $n = 16$ , obtained from the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts) are summarized in the Appendix. Also summarized in the appendix are the equations drawn from Birkebak (1966), which were used to calculate metabolic heat production. For these equations, a heat transfer coefficient ( $k$ ) of 0.102 cal/cm<sup>2</sup>°C was used for the entire body surface (Calder and King 1974). The thermal conductance of Common Eider (*Somateria mollissima*) in water (i.e., wet thermal conductance) has been shown to be 57% greater than it is in the air (Jenssen et al. 1989); therefore, we used a heat transfer coefficient of 0.160 cal/cm<sup>2</sup>°C to calculate heat loss from the ventral body surface to the water. Metabolic heat production was calculated as:  $BMR + Q_{head} + Q_{neck} + Q_{breast} + Q_{body} + Q_{ventral\ surface}$ , where BMR is basal metabolic rate and  $Q$  is the heat loss term for each body component.

Estimates of additional energetic costs resulting from specific daily activities ( $EE_{Activity}$ ) were calculated by multiplying the proportion of time spent in a particular activity by the energetic cost of that activity. We used previously reported multiples of BMR, summarized in Table 1, to calculate the energetic costs of activities by multiplying the propor-

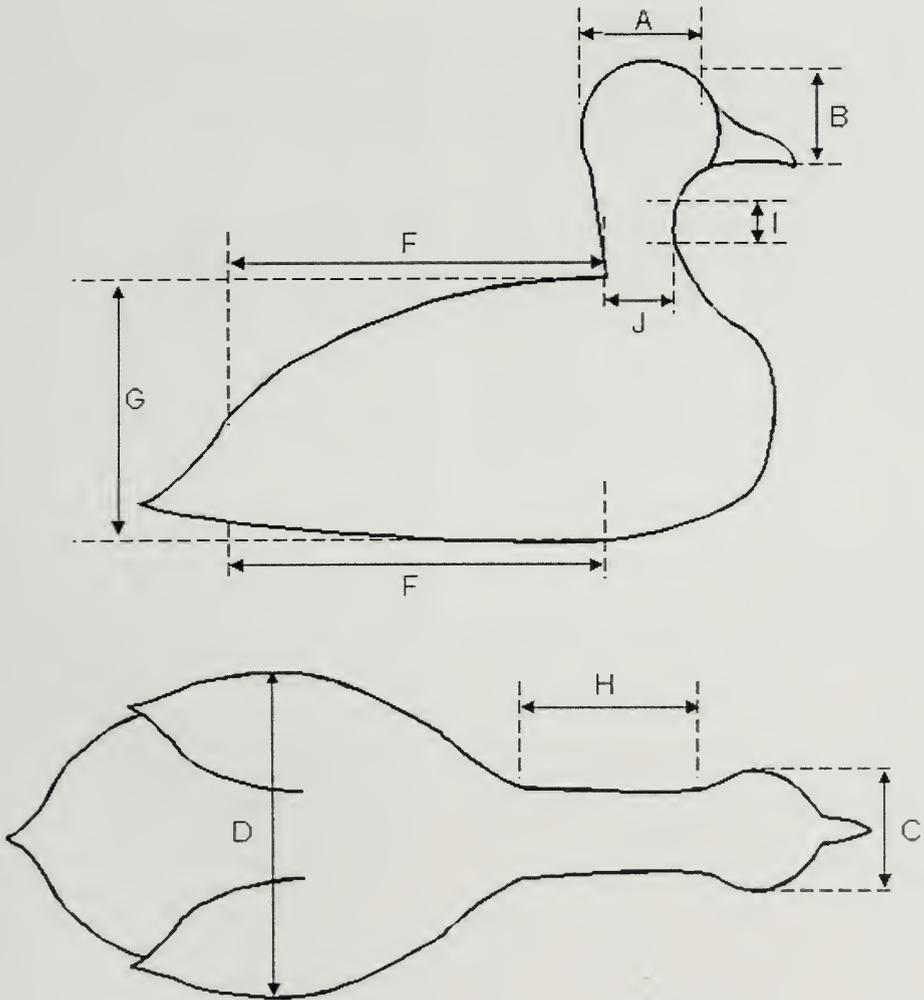


FIG. 1. Body dimension measurement points required for input into the SST model to estimate DEE (see Appendix). A = head length, B = head height, C = head width, D = body width, F = body length, G = body height, H = neck length, I = neck width, J = neck height.

TABLE 1. Energetic costs as a multiple of basal metabolic rate (BMR) of activities used in the site-specific and fixed-cost thermoregulation DEE models.

Activity	Operational definition	Multiple of BMR	Reference
Dive	Diving for food	5.1	de Leeuw 1996
Surface	Surface and pause between dives	5.1	de Leeuw 1996
Look	Peering through the water at the cove bottom	1.8	Wooley and Owen 1978
Courtship	Social display toward individual of the opposite gender	2.4	Albright et al. 1983
Agonistic	Hostile interaction between two individuals	1.8	Wooley and Owen 1978
Swim	Locomotion	3.5	Butler 2000
Fly	Locomotion	12.5	Wooley and Owen 1978
Preen	Maintenance of feathers	2.1	Albright et al. 1983
Alert	Not moving, but actively observing surroundings	1.8	Wooley and Owen 1978
Rest	Not moving with bill tucked in feathers	1.4	Wooley and Owen 1978

tion of time spent in that activity by the corresponding multiple of BMR. The contribution of physical activity to DEE (Table 2;  $EE_{\text{Activity}}$ ) was then calculated by summing the energetic costs of all activities in which Buffleheads engaged.

*DEE fixed-cost thermoregulation model.*—Estimates of DEE were calculated using a method that incorporates a fixed cost of thermoregulation (fixed-cost model; Morton et al. 1989). In this model, the thermoregulatory component ( $EE_{\text{Thermoreg}}$ ) is fixed and estimated at 5.9 kJ/hr (Morton et al. 1989). Additional energetic costs resulting from specific daily activities ( $EE_{\text{Activity}}$ ) were calculated as in the SST model by multiplying the proportion of time spent in a particular activity by the energetic cost of that activity. These two components were then summed to arrive at fixed-cost model estimates of DEE.

*DEE-habitat correlations.*—We identified six Bufflehead wintering habitats within well-defined coves or embayments of the Narragansett Bay estuary. Included were two mesotrophic, rocky- and sandy-bottom embayments (Sheffield Cove: 41° 29' 41" N, 71° 22' 89" W; and Mackerel Cove: 41° 29' 28" N, 71° 20' 86" W), two mesotrophic soft-bottom coves (Coggeshal Cove: 41° 39' 32" N, 71° 20' 52" W; and Brush Neck Cove: 41° 41' 47" N, 71° 24' 48" W), and two eutrophic soft-bottom coves (Apponaug Cove: 41° 41' 40" N, 71° 28' 58" W; and Watchemoket Cove 41° 48' 00" N, 71° 22' 75" W). Cove areas ranged from 18.6 to 86.1 ha, with an average of 42.2 ha. Each cove supported consistent numbers of Buffleheads throughout the winter (November through April); the median flock size at the six sites (determined by bimonthly censuses during the winters of 2001–2002 and 2002–2003) was 18, ranging from 13 to 41. In winter, Buffleheads spend the majority of their time on the water and tend to favor shallow water habitats (<3 m) in protected coves (Stott and Olson 1973, Gauthier 1993). They feed by diving to the cove bottom where they consume benthic invertebrates including crustaceans, gastropods, and bivalves (Yocum and Keller 1961, Wiemeyer 1967, Gauthier 1993).

We used focal animal sampling to quantify activities of Buffleheads at each of the study sites during the winters of 2001–2002 and 2002–2003 (Altmann 1974). We completed

965 observations on individual birds, resulting in over 80 hr of activity budget data. Observations were randomly distributed over sample sites and time during the daytime throughout the winter period when ducks were present (November–April). We chose individual ducks at random (i.e., observations began with the  $i$ th duck from the left in each flock, where  $i$  was a randomly generated number) and observed through a 32–60× spotting scope or through 10 × 50 binoculars for 5 min; behaviors were categorized as dive, surface, look (i.e., peering through the water at the cove bottom), courtship, agonistic, swim, fly, preen, alert, and rest (Table 1). Preening included wing flapping, stretching, and scratching. Gender for each individual was identified when possible, except in rare instances when we were unable to distinguish between females and first-year males that had not yet developed breeding plumage (Carney 1992). Therefore, we report results for “males” (showing breeding plumage) and “females” (includes first year males). Activity data were collected using an observational software program installed on a laptop computer (JWatcher, Animal Behaviour Laboratory, Macquarie University, Australia; <http://www.jwatcher.ucla.edu/>). Prior to analysis, data were aggregated into the following categories: feeding (dive, surface, look), social (courtship, agonistic), locomotion (swim, fly), maintenance (preen, alert), and resting. Each sampling event at a site consisted of 20–30 five-min observations; final data were averaged by sampling event and by site.

*Sensitivity analysis.*—We used linear regression analysis of SST model estimates of DEE versus wind speed and feeding behavior, respectively, to assess the relative contribution of each to DEE. First, we estimated DEE using average values of feeding activity across all sites, and plotted DEE versus wind speed over the range of wind speeds recorded during the study (i.e., feeding activity held constant, wind speed varied; regression equation:  $DEE = [1.1 \times \text{wind speed}] + 42.1$ ). Second, we estimated DEE using average wind speed and temperature across the sites and plotted DEE versus the proportion of feeding activity (i.e., wind speed held constant, feeding activity varied; regression equation:  $DEE = [43.1 \times \text{proportion of time spent feeding}] + 17.3$ ). In each

TABLE 2. Thermoregulatory costs ( $EE_{Thermoreg}$ ), energetic costs resulting from specific daily activities ( $EE_{Activity}$ ), and daily energy expenditure (DEE) of Buffleheads at six winter habitats in Narragansett Bay, Rhode Island, 2001–2003. Values were calculated using thermoregulatory costs based on site-specific temperature and wind speed (site-specific thermoregulation model), and a previous method using fixed thermoregulatory costs (fixed-cost thermoregulation model; Morton et al. 1989). Values are in kJ/hr  $\pm$  SD.

Site <sup>a</sup>	Gender	Site-specific thermoregulation			Fixed-cost thermoregulation		
		$EE_{Thermoreg}$	$EE_{Activity}$	DEE	$EE_{Thermoreg}$	$EE_{Activity}$	DEE
APPCV	Male	10.5 $\pm$ 1.0	39.2 $\pm$ 1.8	49.7 $\pm$ 2.8	5.9	39.2 $\pm$ 1.8	45.1 $\pm$ 2.8
	Female	12.1 $\pm$ 1.1	36.0 $\pm$ 0.8	48.1 $\pm$ 1.9	5.9	36.0 $\pm$ 0.8	41.9 $\pm$ 1.9
	Combined	11.1 $\pm$ 1.1	37.6 $\pm$ 4.1	48.9 $\pm$ 5.2	5.9	37.6 $\pm$ 4.1	43.5 $\pm$ 5.2
BRUCV	Male	9.3 $\pm$ 0.8	37.2 $\pm$ 4.0	46.5 $\pm$ 4.8	5.9	37.2 $\pm$ 4.0	43.1 $\pm$ 4.8
	Female	10.7 $\pm$ 1.0	36.5 $\pm$ 3.5	47.2 $\pm$ 4.5	5.9	36.5 $\pm$ 3.5	42.4 $\pm$ 4.5
	Combined	10.0 $\pm$ 1.0	36.9 $\pm$ 8.5	46.9 $\pm$ 9.5	5.9	36.9 $\pm$ 8.5	42.8 $\pm$ 9.5
COGCV	Male	11.8 $\pm$ 1.1	36.1 $\pm$ 3.9	47.9 $\pm$ 5.0	5.9	36.1 $\pm$ 3.9	42.0 $\pm$ 5.0
	Female	13.7 $\pm$ 1.3	36.0 $\pm$ 5.0	49.7 $\pm$ 6.3	5.9	36.0 $\pm$ 5.0	41.9 $\pm$ 6.3
	Combined	12.8 $\pm$ 1.2	36.1 $\pm$ 8.7	48.8 $\pm$ 9.9	5.9	36.1 $\pm$ 8.7	42.0 $\pm$ 9.9
MAKCV	Male	12.6 $\pm$ 1.2	38.3 $\pm$ 4.2	50.9 $\pm$ 5.4	5.9	38.3 $\pm$ 4.2	44.2 $\pm$ 5.4
	Female	14.7 $\pm$ 1.4	39.2 $\pm$ 5.3	53.9 $\pm$ 6.7	5.9	39.2 $\pm$ 5.3	45.1 $\pm$ 6.7
	Combined	13.7 $\pm$ 1.3	38.8 $\pm$ 7.0	52.4 $\pm$ 8.3	5.9	38.8 $\pm$ 7.0	44.7 $\pm$ 8.3
SHFCV	Male	9.6 $\pm$ 0.9	38.8 $\pm$ 1.4	48.4 $\pm$ 2.3	5.9	38.8 $\pm$ 1.4	44.7 $\pm$ 2.3
	Female	11.2 $\pm$ 1.1	36.3 $\pm$ 7.0	47.5 $\pm$ 8.1	5.9	36.3 $\pm$ 7.0	42.2 $\pm$ 8.1
	Combined	10.4 $\pm$ 1.0	37.5 $\pm$ 8.5	47.9 $\pm$ 9.5	5.9	37.5 $\pm$ 8.5	43.4 $\pm$ 9.5
WATCV	Male	11.7 $\pm$ 1.1	37.6 $\pm$ 2.9	49.3 $\pm$ 4.0	5.9	37.6 $\pm$ 2.9	43.5 $\pm$ 4.0
	Female	12.3 $\pm$ 1.2	35.9 $\pm$ 3.3	48.2 $\pm$ 4.5	5.9	35.9 $\pm$ 3.3	41.8 $\pm$ 4.5
	Combined	12.0 $\pm$ 1.1	36.8 $\pm$ 7.0	48.8 $\pm$ 8.1	5.9	36.8 $\pm$ 7.0	42.7 $\pm$ 8.1
All sites	Male	10.9 $\pm$ 1.0	37.9 $\pm$ 3.0	48.8 $\pm$ 4.1	5.9	37.9 $\pm$ 3.0	43.8 $\pm$ 4.1
	Female	12.5 $\pm$ 1.2	36.7 $\pm$ 4.2	49.1 $\pm$ 5.3	5.9	36.7 $\pm$ 4.2	42.6 $\pm$ 5.3
	Combined	11.7 $\pm$ 1.1	37.3 $\pm$ 7.3	49.0 $\pm$ 8.4	5.9	37.3 $\pm$ 7.3	43.2 $\pm$ 8.4
Correlations with wind speed	Male	—	—	$P = 0.046$	—	—	—
	Female	$P = 0.067$	—	$P = 0.055$	—	—	—
	Combined	—	—	$P = 0.023$	—	—	—

<sup>a</sup> APPCV = Apponaug Cove; BRUCV = Brush Neck Cove; COGCV = Coggeshall Cove; MAKCV = Mackerel Cove; SHFCV = Sheffield Cove; WATCV = Watchemoket Cove.

case, we used average values of temperature and all other activities in the model. Regression equations generated from each analysis were used to estimate the relative contribution of wind speed and feeding behavior to DEE. For wind speed, we calculated the average percent increase in DEE per 1 m/sec increase in wind speed. For proportion of time spent feeding, we calculated the average percent increase in DEE per 5% increase in the proportion of time spent feeding.

**Statistical analyses.**—Differences in the proportion of time spent on different activities by males versus females were investigated using two-tailed Student's *t*-tests on data averaged across all sample sites. Site-specific time budgets were calculated by averaging individual observations by sampling event and then by averaging sampling events by site. Proportions were arcsine-square-root transformed prior to regression analysis (Fowler et al. 1998:87–88). Wind speed and temperature were averaged by sampling event and by site. Regression analysis and analysis of variance were used to assess the influence of environmental conditions on DEE and feeding behavior. Statistical analyses were performed using SAS (SAS Institute, Inc. 2001).

## RESULTS

Estimates of DEE for wintering Buffleheads generated using the SST model averaged  $49.0 \pm 8.4$  kJ/hr, or  $1,176 \pm 202$  kJ/day, and differed by up to 12% among sites (Table 2). The mean thermoregulatory component of DEE ( $EE_{\text{Thermoreg}}$ ; Table 2) was  $11.7 \pm 1.1$  kJ/hr or 23.9% of total DEE;  $EE_{\text{Thermoreg}}$  increased with increasing wind speed ( $r^2 = 0.61$ ,  $P = 0.067$ ). DEE did not differ between males and females; however, thermoregulatory costs were higher for females (mean =  $12.5 \pm 1.2$  versus  $10.9 \pm 1.0$  kJ/hr for males;  $t_5 = -7.2$ ,  $P < 0.001$ ).

The mean DEE (all sites) calculated using the SST model was 13.4% higher than that calculated using the fixed-cost model (Table 2). The thermoregulatory component of DEE, 5.9 kJ/hr, composed 13.7% of total DEE calculated with the fixed-cost model.

Daily energy expenditures of Buffleheads calculated with the SST model increased with increasing wind speed for males ( $r^2 = 0.67$ ,  $P = 0.046$ ), females ( $r^2 = 0.64$ ,  $P = 0.055$ ), and

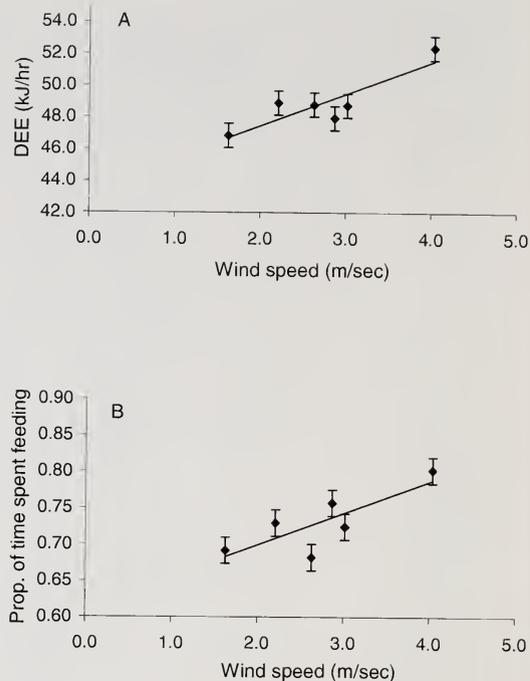


FIG. 2. Correlation of wind speed with (A) DEE and (B) time spent feeding for Buffleheads (males and females combined) wintering at six coastal habitats in Narragansett Bay, Rhode Island, 2001–2003. Wind speeds are means of all sampling sessions conducted at a site. Error bars are  $\pm$  SE.

males and females combined ( $r^2 = 0.76$ ,  $P = 0.023$ ; Fig. 2A). The proportion of time spent feeding by Buffleheads also increased with increasing wind speed ( $r^2 = 0.67$ ,  $P = 0.047$  Fig. 2B). Estimates of DEE that were generated using the fixed-cost model showed no relationship between DEE and wind speed.

Buffleheads spent  $75.7 \pm 4.3\%$  of their time feeding during daylight hours, and females fed more often than males ( $77.1 \pm 5.4\%$  versus  $74.2 \pm 6.9\%$ ;  $t_{545} = -2.6$ ,  $P = 0.004$ ; Table 3). Males, however, spent more of their time engaged in courtship activities (2.39% versus 0.43%;  $t_{545} = 7.4$ ,  $P < 0.001$ ). Males and females (combined) averaged 16.8% of their time engaged in locomotion and maintenance, and 4.5% of the time resting (Table 3). Buffleheads at Mackerel Cove spent the greatest proportion of time feeding and the least in all other activities, whereas those at Coggeshal Cove spent the least time feeding and the most in all other activities, except resting. Overall, Buffleheads spent between 0.3 and 2.6% of

TABLE 3. Time spent (mean percent ± SD) by Buffleheads in different activities, average ambient temperature (°C), and wind speeds (m/sec) at six winter habitats in Narragansett Bay, Rhode Island, 2001–2003. Time budget data were averaged by sampling event and by site.

Site <sup>a</sup>	Gender	Bufflehead activity					Ambient temperature	Wind speed
		Feeding	Social	Locomotion	Maintenance	Resting		
APPCV	Male	66.6 ± 5.4	1.84 ± 2.15	12.7 ± 3.6	11.0 ± 6.5	4.65 ± 1.80	4.5	2.2
	Female	80.1 ± 0.9	0.55 ± 0.11	9.49 ± 1.86	4.76 ± 0.94	2.74 ± 0.54		
	Combined	73.3 ± 3.2	1.20 ± 1.13	11.1 ± 2.7	7.89 ± 3.69	3.70 ± 1.17		
BRUCV	Male	72.4 ± 12.6	3.89 ± 2.10	11.8 ± 5.2	9.25 ± 3.64	5.01 ± 4.67	6.2	1.6
	Female	73.0 ± 3.6	1.37 ± 1.58	9.78 ± 4.68	7.11 ± 3.32	4.34 ± 2.11		
	Combined	72.7 ± 8.1	2.63 ± 1.84	10.8 ± 4.9	8.18 ± 3.48	4.67 ± 3.98		
COGCV	Male	78.3 ± 12.7	4.05 ± 1.74	14.0 ± 5.0	9.89 ± 4.71	4.94 ± 0.19	1.6	2.6
	Female	68.7 ± 11.4	0.18 ± 0.14	12.9 ± 3.3	9.49 ± 4.72	5.92 ± 3.75		
	Combined	73.5 ± 16.3	2.11 ± 0.94	13.4 ± 4.2	9.69 ± 4.70	5.43 ± 1.97		
MAKCV	Male	85.5 ± 12.6	0.43 ± 0.74	5.14 ± 0.58	1.71 ± 2.17	2.82 ± 1.66	3.4	4.0
	Female	81.1 ± 8.7	0.18 ± 0.29	6.77 ± 1.35	5.73 ± 4.26	2.01 ± 2.55		
	Combined	83.3 ± 11.4	0.30 ± 0.52	5.95 ± 0.97	3.72 ± 3.21	2.42 ± 2.10		
SHFCV	Male	73.8 ± 3.5	1.78 ± 1.78	6.60 ± 5.31	9.01 ± 5.15	5.46 ± 4.53	9.1	2.9
	Female	82.8 ± 11.4	0.14 ± 0.22	5.69 ± 5.07	3.83 ± 3.14	3.84 ± 4.06		
	Combined	78.3 ± 7.5	0.96 ± 1.00	6.14 ± 5.19	6.42 ± 4.14	4.65 ± 4.30		
WATCV	Male	68.6 ± 10.0	2.33 ± 1.66	12.2 ± 5.3	8.08 ± 2.32	7.02 ± 2.96	6.7	3.0
	Female	77.2 ± 7.2	0.18 ± 0.16	7.68 ± 4.49	6.53 ± 0.87	5.48 ± 2.65		
	Combined	72.9 ± 8.6	1.26 ± 0.91	9.91 ± 4.89	7.31 ± 1.60	6.25 ± 2.80		
All sites	Male	74.2 ± 6.9	2.39 ± 1.38	10.4 ± 3.6	8.16 ± 3.31	4.98 ± 1.35	5.2	2.7
	Female	77.1 ± 5.4	0.43 ± 0.48	8.71 ± 2.57	6.24 ± 1.98	4.05 ± 1.51		
	Combined	75.7 ± 4.3	1.41 ± 0.83	9.55 ± 2.95	7.20 ± 2.02	4.52 ± 1.34		
Correlations with wind speed		—	—	—	—	—	—	—
Correlations with feeding		—	—	—	—	—	—	—
			$P = 0.067$					
			$P = 0.043$					
								$P = 0.001$

<sup>a</sup> APPCV = Apponaug Cove; BRUCV = Brush Neck Cove; COGCV = Coggeshall Cove; MAKCV = Mackerel Cove; SHFCV = Sheffield Cove; WATCV = Watchemoket Cove.

their time in social activities, and this time decreased as the ducks increased feeding ( $r^2 = 0.71$ ,  $P = 0.043$ ). Similarly, the amount of time spent in maintenance activities (range = 3.7–9.7%) decreased as time spent feeding increased ( $r^2 = 0.96$ ,  $P = 0.001$ ).

Sensitivity analysis of model estimates of DEE versus wind speed at constant proportion of time spent feeding showed that a 1 m/sec increase in wind speed resulted in a 2.5% increase in DEE. Analysis of DEE versus the proportion of time spent feeding at constant wind speed showed that a 0.05 increase in proportion of time spent feeding resulted in a 4.5% increase in DEE.

## DISCUSSION

Our estimates of DEE using the SST model for Buffleheads at the Narragansett Bay wintering sites ( $1,175 \pm 202$  kJ/day) are higher than those predicted from the fixed-cost model ( $1,036 \pm 202$  kJ/day), which uses a single energetic cost of thermoregulation. Thermoregulatory costs predicted by the SST model constitute up to 28% of the animal's total DEE and are approximately twice as high on average as that used in the fixed-cost model. DEE estimates for Buffleheads at our sites were also higher than a field metabolic rate predicted by an allometric relation of energy expenditure based on empirical studies (606 kJ/day, non-passerines; Nagy et al. 1999). However, many of the studies from which this relation was derived were carried out in the breeding season in warm ambient temperatures, so our higher DEE estimates may be attributed in part to environmental conditions and the inclusion of thermoregulatory energy costs.

Our model does not include the contribution of heat gained from solar radiation or heat lost through evaporative water loss because these effects are likely relatively small (less than 10% of heat loss; Scholander et al. 1950, Strunk 1971, Wolf and Walsberg 2000), and were likely similar between our study sites. Nonetheless, these constraints limit the application of our model to comparative, single-species studies between habitats that are located in a similar geographic region. It is also important to note that the SST model is limited by the availability of empirically derived energetic equivalents of specific waterfowl be-

haviors, as is the fixed-cost model. We applied the model to Buffleheads, but were restricted to using literature-based energetic equivalents that were not specific to that species. Therefore, the DEE estimates presented here, while higher than those calculated from the fixed-cost model and from body mass alone, fall well within the probable error of 20–40% proposed by Weathers et al. (1984) for models that rely on generic energetic equivalents. However, while it would be difficult to argue that our model estimates are more accurate than those calculated from fixed-cost or body mass models, the utility of our model lies in the ability to determine the relative contribution of wind speed, temperature, and specific waterfowl behaviors to DEE across sites with different environmental conditions and levels of activity.

Wintering waterfowl may incur substantial thermoregulatory costs depending on ambient temperatures and the combined effect of wind and cold, and these may lead to increases in DEE. Changes in the relative amounts of activities exhibited by wintering Buffleheads may also alter DEE. In our study, estimates of DEE calculated with the SST model were correlated with wind speed (Fig. 2A). However, feeding activity also increased with increasing wind speed (Fig. 2B), which could also contribute to an increase in DEE. Sensitivity analysis of the effects of increases in wind speed and feeding activity on DEE showed that increases in feeding activity resulted in a relative increase in waterfowl DEE nearly twice that of a corresponding increase in wind speed. Feeding activity may increase because of decreased prey abundance, or because of changes in the availability or energetic content of prey. Further studies at our sites have shown that feeding activity increased with decreasing prey abundance, and also with decreasing prey energy density resulting from changes in available prey species at a site and inter-specific differences in the energetic content of prey (RAM and SRM unpubl. data). However, other factors, such as intra- and inter-specific competition and increased energetic demands, may also influence the amount of feeding activity. Although we are uncertain as to the cause of increases in time spent feeding at our sites, our results show that increased

feeding activity may have a greater impact than wind exposure on DEE of Buffleheads.

Increased feeding activity may also affect the short- and long-term survival of Buffleheads. For example, if wintering Buffleheads need to spend more time feeding, time for other activities such as courtship and pair formation may be limited (Drent and Daan 1980, Meijer and Drent 1999). Although they exhibit long-term pair bond formation and a high degree of flock synchrony, which results in a relatively small proportion of time spent in social behaviors, courtship and maintenance activities are still important for their overall reproductive success (Robertson et al. 1998). Our results indicate that as Buffleheads at our sites spent more time feeding, they had less time available for maintenance and social behaviors, which may have an impact on both their short- and long-term survival. This, coupled with the greater increases in energetic costs due to feeding activity predicted from model sensitivity analysis, suggests that DEE of wintering waterfowl in harsh climates would be lower in habitats with both high prey density and adequate protection from exposure. For example, sites such as Brush Neck Cove, which had the highest prey abundance (RAM and SRM unpubl. data) and also the lowest thermoregulatory costs for Buffleheads (Table 2), may be better candidate sites for protection as waterfowl wintering habitats compared with sites such as Mackerel Cove, which had low prey abundance and high thermoregulatory costs.

In summary, our SST model estimated DEE as the sum of basal metabolic rate and site-specific energetic costs of activity and thermoregulation. The primary benefits of the SST model compared to other approaches include its ability to (1) evaluate the effect of thermoregulatory costs on DEE of wintering waterfowl using simple measurements of wind speed and ambient temperature, (2) predict the extent to which the behavior of waterfowl during winter affects DEE, and (3) track changes in DEE over different time scales (i.e., hourly, daily, or seasonally) if the corresponding activity and environmental data are available. Also, because of its ability to estimate site-specific DEE based on local conditions, the model may be useful in evaluating the quality of waterfowl habitats that have different attri-

butes such as prey abundance, or degree of protection from high winds and extreme temperatures. However, further studies will be needed to establish the independence of behavioral responses to environmental conditions from the primary effect of the conditions themselves on the DEE of resident waterfowl before model estimates can be used in habitat assessment.

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APPENDIX. Variables used to calculate heat transfer, an adjusted metabolic rate at ambient temperature, using a heat transfer model proposed by Birkebak (1966). Representative values are from repeated measurements on live and preserved Buffleheads from northeastern estuaries. Equations are taken from Birkebak (1966);  $k$  is the heat transfer coefficient,  $\Delta T$  is the difference between body temperature (39° C) and ambient temperature.

Variable	Symbol	Equation	Representative value (cm ± SD)
Head length	A	—	5.9 ± 0.4
Head height	B	—	5.0 ± 0.8
Head width	C	—	3.2 ± 0.4
Body width	D	—	9.1 ± 0.9
Body length	F	—	18.2 ± 1.1
Body height	G	—	6.3 ± 0.6
Neck length	H	—	2.0 ± 0.3
Neck width	I	—	2.9 ± 0.4
Neck height	J	—	2.9 ± 0.4
Integument depth-body	$\Delta X_{\text{body}}$	—	0.4 ± 0.1
Integument depth-head	$\Delta X_{\text{head}}$	—	0.7 ± 0.2
Integument depth-neck	$\Delta X_{\text{neck}}$	—	0.7 ± 0.2
Inner radius of body	$r_{i \text{ body}}$	$r_{i \text{ body}} = (D + G)/4$	3.9 ± 0.5
Inner radius of head	$r_{i \text{ head}}$	$r_{i \text{ head}} = (B + C)/4$	2.1 ± 0.4
Inner radius of neck	$r_{i \text{ neck}}$	$r_{i \text{ neck}} = (I + J)/2$	2.9 ± 0.6
Length of body	$L_{\text{body}}$	$L_{\text{body}} = F - (D + G)/2$	10.5 ± 0.5
Length of neck	$L_{\text{neck}}$	$L_{\text{neck}} = H - (I + J)/2$	0.9 ± 0.1
Outer radius of body	$r_{o \text{ body}}$	$r_{o \text{ body}} = r_{i \text{ body}} + \Delta X_{\text{body}}$	4.6 ± 0.8
Outer radius of head	$r_{o \text{ head}}$	$r_{o \text{ head}} = r_{i \text{ head}} + \Delta X_{\text{head}}$	2.8 ± 0.7
Outer radius of neck	$r_{o \text{ neck}}$	$r_{o \text{ neck}} = r_{i \text{ neck}} + \Delta X_{\text{neck}}$	6.8 ± 1.1
Area of ventral surface	$A_{\text{vs}}$	$A_{\text{vs}} = L_{\text{body}} \times 2r_{o \text{ body}}$	96.0 ± 21.6
Heat loss from head	$Q_{\text{head}}$	$Q_{\text{head}} = (2\pi \times r_{o \text{ head}} \times r_{i \text{ head}} \times k \times \Delta T) / (r_{o \text{ head}} - r_{i \text{ head}})$	—
Heat loss from neck	$Q_{\text{neck}}$	$Q_{\text{neck}} = (2\pi \times L_{\text{neck}} \times k \times \Delta T) / [\ln(r_{o \text{ neck}}/r_{i \text{ neck}})]$	—
Heat loss from breast	$Q_{\text{breast}}$	$Q_{\text{breast}} = (2\pi \times r_{o \text{ body}} \times r_{i \text{ body}} \times k \times \Delta T) / (r_{o \text{ body}} - r_{i \text{ body}})$	—
Heat loss from body	$Q_{\text{body}}$	$Q_{\text{body}} = (2\pi \times L_{\text{body}} \times k \times \Delta T) / [\ln(r_{o \text{ body}}/r_{i \text{ body}})]$	—
Heat loss from ventral surface	$Q_{\text{vs}}$	$Q_{\text{vs}} = k \times A_{\text{vs}} \times (T_b - T_a)$	—
Heat loss from tail	$Q_{\text{tail}}$	$Q_{\text{tail}} = Q_{\text{breast}}$	—

## APPARENT PREDATION BY CATTLE AT GRASSLAND BIRD NESTS

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**ABSTRACT.**—We document the first cases of cattle behaving as avian predators, removing nestlings and eggs from three active ground nests in continuously grazed pastures in southwestern Wisconsin, 2000–2001. Cows removed three of four Savannah Sparrow (*Passerculus sandwichensis*) eggs from one nest (the fourth egg was damaged), all four Eastern Meadowlark (*Sturnella magna*) nestlings from another, and all three Savannah Sparrow nestlings from a third. We found only two of three missing eggs (intact) and one of seven missing nestlings (dead) near two of the nests. Cows may have eaten the egg and nestlings we were unable to account for; alternatively, the egg and nestlings may have been scavenged by predators or removed from the area by the adult birds. Without videotape documentation, we would have attributed nest failure to traditional predators and cattle would not have been implicated. We may be underestimating the impact of cattle on ground nests by not considering cattle as potential predators. Received 10 May 2004, accepted 6 December 2004.

Over the last 30 years, grassland birds have declined more rapidly and consistently than any other avian guild in the Midwest (Vickery and Herkert 2001). One possible cause is the loss and fragmentation of native and secondary grasslands (Sample et al. 2003). Herkert et al. (1996) found a significant correlation between the decline of grassland birds in the Midwest and the conversion of hay and pasture acreage to row crops and other unsuitable habitat. Since the conversion of land from native prairie to agriculture during European settlement, secondary grasslands, such as pastureland, have become critical components of grassland passerine conservation (Herkert 1991, Herkert et al. 1996, Sample and Mossman 1997).

Nest predation is a major factor in the nesting failure of most passerine species (Lack 1968, Ricklefs 1969, Martin 1988). This may be a particular problem in grassland ecosystems where generalist predators, such as raccoons (*Procyon lotor*) and skunks (*Mephitis* spp.), have responded positively to human disturbance and landscape fragmentation (Sargeant et al. 1993, Warner 1994). In actively grazed pastures, ground-nesting grassland birds face additional risks from cattle. In southwestern Wisconsin, Temple et al. (1999) thought that many of the nest losses incurred

by grassland birds in grazed pastures were a result of cattle trampling and nest desertion after cattle had grazed down the vegetation surrounding the nest.

In previous literature on cattle disturbance to bird nests, authors have used sign to interpret the occurrence of cattle disturbance, mainly at artificial nests and under rotational grazing regimes (Paine et al. 1996, 1997). Under a rotational grazing regime at the University of Wisconsin's Lancaster Agricultural Research Station in southwestern Wisconsin, Paine et al. (1996) documented cattle disturbance resulting in nest failure at simulated ground nests in which Ring-necked Pheasant (*Phasianus colchicus*) eggs had been placed. Ninety-four percent of failed nests were the result of cattle damage. Nest disturbance included nest contents being trampled, kicked out, crushed by the animal's muzzle, or covered with a manure pile. The mean percentage of nests ( $n = 15$ ) having  $\geq 1$  egg trampled by a bovine hoof was 63% for the 1-day treatment, 52% for the 4-day treatment, and 41% for the 7-day treatment.

In a refinement of their 1996 study, Paine et al. (1997) documented cattle sniffing, licking, and occasionally picking up contents of simulated ground nests (clay pigeon targets and pheasant eggs). Their study was not designed to represent natural conditions, but rather to assess intentional and inadvertent nest disturbances. Overall trampling levels for clay pigeon targets and pheasant eggs were 35 and 36%, respectively. Cattle intentionally disturbed 25% of clay targets and 8% of egg

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nesses. In a few instances, cattle picked up single eggs with their mouths and carried them "several feet" without damaging them.

Whereas several studies have evaluated cattle trampling and/or disturbance at artificial ground nests in rotationally grazed pastures (Koerth et al. 1983; Jensen et al. 1990; Paine et al. 1996, 1997), few studies have documented cattle disturbances to nests in continuously grazed systems under conditions occurring in the Midwest.

Cattle have not previously been documented deliberately removing eggs and young from active passerine nests. Other herbivores that have been documented eating or removing eggs and/or young include white-tailed deer (*Odocoileus virginianus*; Pietz and Granfors 2000) and caribou (*Rangifer tarandus*; Abraham et al. 1977) in North America, and sheep (*Ovis*) and red deer (*Cervus elaphus*) in the British Isles (Furness 1988a, 1988b; Pennington 1992). Our study is unique in providing direct documentation of cattle effects on real nests of grassland passerines under a continuous grazing regime.

## METHODS

We searched for ground-nesting grassland bird nests in continuously grazed pastures in 2000 ( $n = 10$ ) and 2001 ( $n = 9$ ) in southwestern Wisconsin (Nack 2002). Stocking rates in pastures (May–August) ranged from 0.61 to 4.28 animal units (AU)/ha (mean = 2.09, SE = 0.37,  $n = 10$ ) and from 0.75 to 4.33 AU/ha (mean = 2.19, SE = 0.34,  $n = 9$ ) in 2000 and 2001, respectively.

To capture video footage of nest predators, we used methods and camera equipment similar to those used by Renfrew and Ribic (2003). Sentinel™ all-weather miniature video camera surveillance systems (Sandpiper Technologies, Manteca, California) were deployed at nests between 15 May and 31 July 2000–2001. In a pilot study during 2000, cameras were placed in a single pasture at 13 of 198 nests. In 2001, cameras were set up in six pastures (including the pasture used in 2000) at 41 of 196 nests. In total, we monitored 54 ground nests with cameras: 34 Savannah Sparrow (*Passerculus sandwichensis*), 12 meadowlark (*Sturnella magna* and *S. neglecta*), 4 Bobolink (*Dolichonyx oryzivorus*), 3 Grasshopper Sparrow (*Ammodramus sava-*

*narum*), and 1 Upland Sandpiper (*Bartramia longicauda*).

Cameras were mounted 5–30 cm above ground on a wooden dowel and placed approximately 12–25 cm from nests. Cameras were concealed in surrounding vegetation in an attempt to avoid detection by predators. Because vegetation height in the pastures was relatively short and birds preferred to nest in small clumps of grass, we were forced to place cameras closer to nests than we would have liked. Each camera's field of view included the nest and a small area surrounding the nest.

Each camera was 4 × 4 × 4 cm (64 cm<sup>3</sup>) in size and had infrared light-emitting diodes (LEDs) mounted around the lens to provide illumination at night. The camera was connected by a 25-m cable to a 24-hr, time-lapse videocassette recorder (VCR) and a deep-cycle marine battery. The cable was buried just underneath the sod layer to protect it from cattle and rodents. The VCR was enclosed in a waterproof case, and the battery and case were covered with a pyramid made from metal hog-fencing panels. The pyramid was then staked into the ground to prevent cattle disturbance and covered with a piece of green canvas to shade the VCR and prevent it from overheating. Nests were checked remotely each day by using a monitor at the VCR to view the nest without having to disturb the nesting birds. The battery powering the VCR was changed every other day and the tape was changed daily. The VCR recorded 4 frames/sec; thus, a standard VHS tape would last for a 24-hr period.

Videotapes were reviewed to determine nest fates and identify predators. We considered a nest successful if one nestling fledged. We used head size, shape, and position to identify images as cattle. We refer to the cattle as cows (pastures were stocked with cows, cow/calf pairs, and one bull).

We categorized nest failure attributed to cattle as either apparent nest predation or inadvertent disturbances (e.g., trampling, knocking the camera into the nest bowl and subsequently breaking eggs). We defined apparent nest predation as the deliberate removal of nest contents by cattle, but with the ultimate fate (i.e., consumption) unknown.

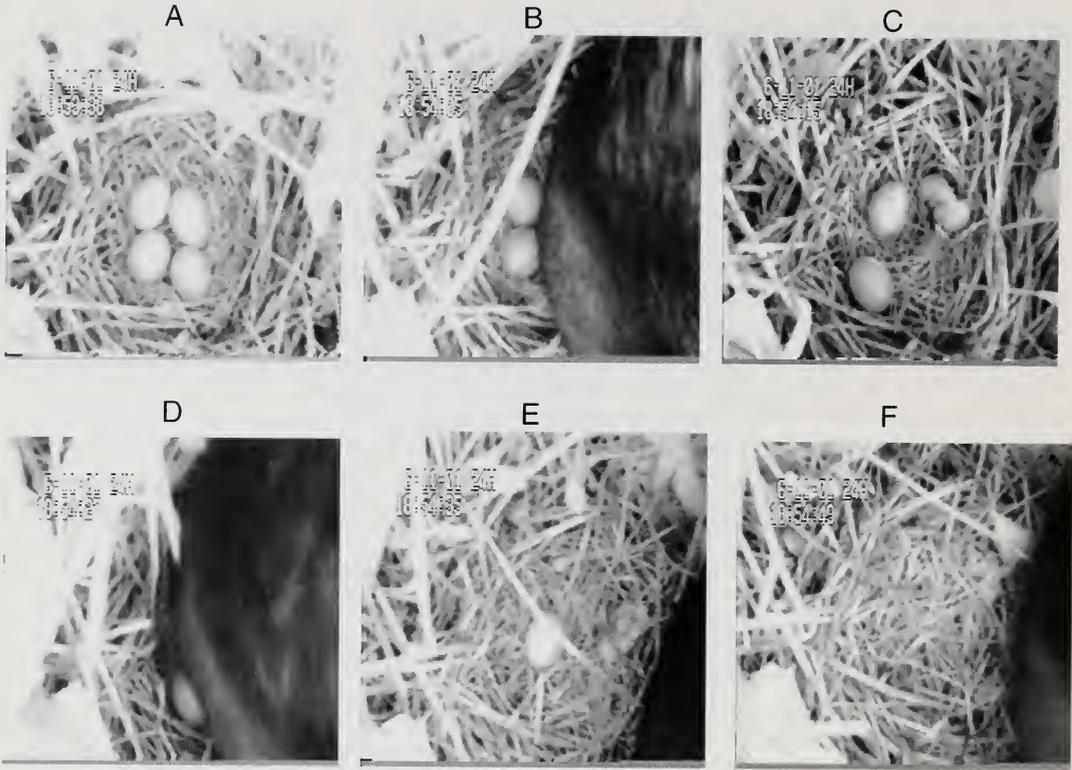


FIG. 1. Sequence of images documenting a cow removing three Savannah Sparrow eggs from an open-cup nest and crushing the fourth egg in a southwestern Wisconsin pasture, 11 June 2001.

## RESULTS

Of the 54 nests monitored by cameras, 7 were abandoned after the camera was deployed, 12 were successful, 21 were depredated by "traditional" predators, and 14 failed due to cattle disturbance. Seven of the 14 (50%) cattle-caused nest failures were inadvertent disturbances; a cow lay down on one nest, one was abandoned, two were trampled, and the camera was knocked down at three nests, crushing the eggs. Apparent nest predation occurred at 3 of the 14 (21%) nests. At four others, we were unable to categorize the nest failure attributed to cattle. In three of these four cases, the camera was either knocked over or tipped by a cow, but there was no clear footage of events; some of the nest contents were missing but we could not be certain they were removed by the cow (they may have been removed by one of the adult birds). In the fourth case, grass was pushed up against the camera and it was unclear whether a cow killed the nestlings with

its muzzle or trampled them. After the cow left, camera footage revealed that an adult bird returned and removed all five dead nestlings.

The following summarizes the three instances of apparent nest predation by cattle.

*Event 1.*—On 11 June 2001 at 18:53:27 CST, an adult Savannah Sparrow flushed from its open-cup nest containing four eggs (Fig. 1A, 18:53:38). The grass surrounding the nest began to move 9 sec later. At 18:54:02, a cow's muzzle was visible at the nest bowl, where it remained for 13 sec (Fig. 1B, 18:54:05). At 18:54:15, the cow moved its muzzle out of the nest and the videotape showed two intact eggs and one broken egg in the nest (Fig. 1C). At 18:54:21, the cow's muzzle was again visible at the nest bowl and remained there for 37 sec (Fig. 1D, 18:54:27), during which time the cow continued to remove eggs. At 18:54:35, there was a clear view of one intact egg and one broken egg (Fig. 1E). At 18:54:49, only a piece of the broken egg was in the nest bowl (Fig. 1F). The cow's muzzle

moved out of view at 18:54:58, but the cow continued to stay near the nest and returned to the empty nest bowl a few times, apparently licking the grass. At 18:56:46, the cow tipped the camera over and nuzzled it until 18:57:45, when the cow presumably left. In summary, the cow was at the nest bowl for at least 50 sec during two visits. After examining the nest bowl and surrounding area, we found two intact eggs approximately 20 cm from the nest and a piece of eggshell in the nest bowl. The nest bowl was slightly pulled apart.

*Event 2.*—On 23 May 2001 at 06:45:07, an adult Eastern Meadowlark left its domed nest after feeding four 5-day-old nestlings. At 07:00:27, grass movement was visible on the videotape and it was apparent that the camera was being nudged. At 07:03:25, a cow put its muzzle in the nest bowl, where it remained for 8 sec before moving out of camera view. At 07:03:33, only three nestlings remained. During the next 6 min, the cow stayed in the area of the nest, as evidenced by grass and camera movement. At 07:09:29, the cow returned and placed its muzzle in the nest bowl for 4 sec. At 07:09:33, there were only two nestlings in the nest (cow not visible in the frame). At 07:11:13, an adult meadowlark returned to the nest with a caterpillar, fed the remaining two nestlings, and sat on the nest. The nest was tended for the next 11 hr (07:09 to 18:07). We inspected the nest area at 14:00 and found no sign of the two missing nestlings; there were still two live nestlings in the nest.

An adult fed the nestlings at 18:07:46 and left at 18:12:16 with a fecal sac. The grass began to move at 18:18:17 and the camera was jostled. At 18:18:28, a cow placed its muzzle in the nest bowl, where it remained for 3 sec. The camera was then moved so that the nest was out of view, but the cow's dark muzzle could be detected occasionally through the vegetation until 18:18:53. In summary, a cow was at the nest for at least 15 sec during three visits. We inspected the nest area again on 24 May at 13:30, and found no young in the nest; however, 30 cm from the nest was a dead nestling that had no visible signs of injury. The edges of the nest bowl were flattened and the camera was turned slightly. In our study area, Eastern Meadow-

larks typically fledge at 10 days, so it is unlikely that the missing nestlings survived.

*Event 3.*—On 7 July 2001 at 05:11:37, an adult Savannah Sparrow fed three 7-day-old nestlings in its open-cup nest. At 05:11:44, the adult left carrying a fecal sac. At 05:15:46, grass movement was detected on the video. At 05:16:03, a cow's muzzle was visible at the nest (Fig. 2A), where it remained for 5 sec, but the cow did not remove any of the nestlings (Fig. 2B, 05:16:21). At 05:16:45, a cow's muzzle passed over the nestlings again for 3 sec without removing anything. At 05:16:53, a cow's muzzle was visible at the nest for a third time for 13 sec, during which time the cow pulled its muzzle out of the nest bowl with at least one nestling in its mouth (presumably two nestlings; Fig. 2C, 05:17:01). The cow then dropped one nestling back into the nest bowl (Fig. 2D, 05:17:02) and moved out of camera view. Two nestlings remained in the nest bowl (Fig. 2E, 05:17:26). At 05:17:30, a cow's muzzle was again visible at the nest bowl and remained there for 5 sec, during which time it removed both of the remaining nestlings (Fig. 2F, G). At 05:17:35, the nest bowl was empty (Fig. 2H). In summary, the cow was at the nest for at least 26 sec during four visits. We examined the nest and surrounding area on 7 July at 12:50, and found no sign of the three nestlings; the nest bowl was flattened on one side and the grass surrounding the nest was trampled. The nestlings showed no attempt to fledge during filming and we think it is unlikely that they survived.

## DISCUSSION

This study was designed to document the predators of ground-nesting grassland bird nests in continuously grazed pastures in southwestern Wisconsin. The use of cameras allowed us to document—for the first time—apparent nest predation by cattle. Cattle removed eggs and nestlings, then either consumed nest contents that were unaccounted for or simply carried them off. Alternatively, missing nest contents may have been scavenged by other animals or removed from the nest area by the adult birds after the cattle left.

All of our pastures were on private land where stocking rates were at the discretion of the landowner. In the Midwest, a light, continuous grazing regime would be about 1

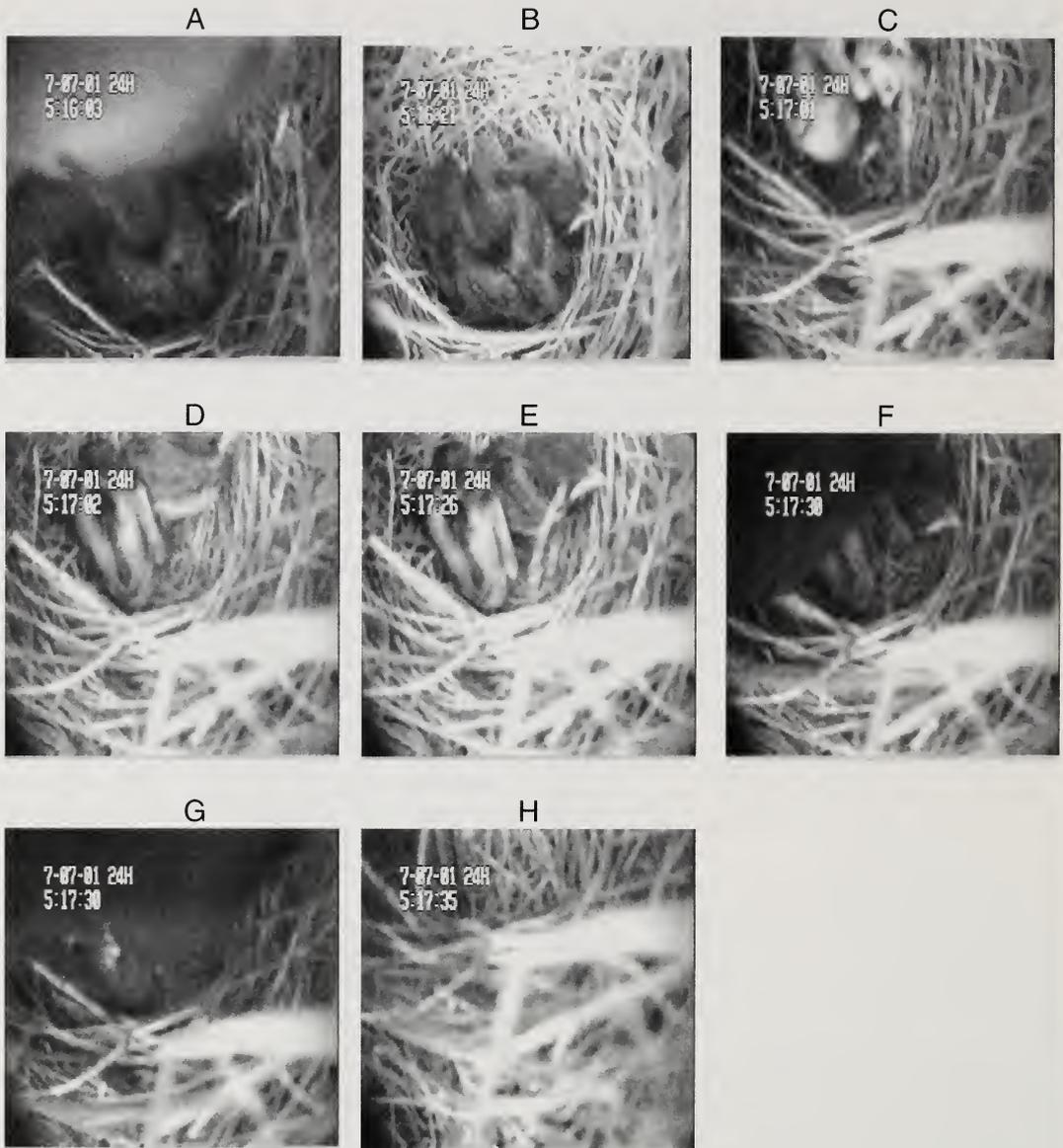


FIG. 2. Sequence of images documenting a cow removing three 7-day-old Savannah Sparrow nestlings from an open-cup nest in a southwestern Wisconsin pasture, 7 July 2001.

AU/ha, and a moderate, continuous grazing regime would be about 2 AU/ha under average environmental conditions (D. J. Undersander pers. comm.). Stocking rates in the pastures we studied appeared to be moderate. Although camera equipment in the pastures may have contributed to cattle disturbance of nests, we do not believe that stocking rates per se influenced cattle disturbance to the cameras or the nests. Instead, cattle-caused nest failure

appeared to be associated more with the behavior of individual herds rather than stocking rates (Nack 2002). Our observations suggest that curiosity and behavior of cattle toward the camera and VCR system varied among herds. The range of behavior we observed was similar to that described by Renfrew and Ribic (2003) in southwestern Wisconsin. In some pastures, cattle were uninterested in camera equipment; they only investigated it initially

and then ignored it. In a few pastures, cattle frequently knocked over the cameras, but did not necessarily cause nests to fail.

Whether or not cattle found nests as a result of their attraction to the cameras, we documented that once a cow discovers a nest, it does not necessarily ignore it. Similar events likely occur when cattle incidentally discover nests while grazing, much like any other predator that forages opportunistically. Based on the evidence (or lack thereof), we would have assigned nest fate correctly as predation, but would not have considered cattle as possible predators. Videotaped evidence of cattle removing nestlings and eggs from ground nests suggests that the impact of cattle on grassland bird nests has been underestimated in the past.

Future studies should be conducted to quantify the extent to which cattle disturb nests while minimizing their attraction to camera equipment. To reduce curiosity and habituate cattle to camera equipment, Renfrew and Ribic (2003) suggest deploying "fake" camera systems 2 to 3 weeks prior to use.

Conducting research on ground-nesting grassland birds in actively grazed pastures is challenging. Future advances in camera technology may benefit researchers. For example, cameras that can be placed in close proximity to nests while providing a wider field of view would help with identifying larger predators and determining the fate of each egg and/or nestling. Wireless camera systems (e.g., King et al. 2001) designed to operate from outside of the pasture fencing would eliminate the need to have the VCR, battery, and protective pyramid, which seem to attract the cattle. This would also reduce set-up time, as there would be no need to bury video cable.

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## INFLUENCE OF FORAGING AND ROOSTING BEHAVIOR ON HOME-RANGE SIZE AND MOVEMENT PATTERNS OF SAVANNAH SPARROWS WINTERING IN SOUTH TEXAS

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**ABSTRACT.**—We used radio telemetry to examine Savannah Sparrow (*Passerculus sandwichensis*) home-range size and foraging and roosting behavior on Padre Island National Seashore in south Texas during January and February, 2002 and 2003. Savannah Sparrows maintained fixed home ranges in winter. Mean home-range size (95% Kernel Home Range [KHR]) was 9.1 ha with a mean core area (50% KHR) of 0.9 ha. Within home ranges, mean foraging and roosting areas were 5.6 and 6.6 ha, respectively. Three distinct habitat types were used by Savannah Sparrows on the island: foredunes (adjacent to the ocean), interior grasslands, and lagoons. Birds using the foredunes had significantly larger home ranges and traveled longer distances between their foraging and roosting locations, always moving inland to roost. Roosting and foraging areas overlapped less for these birds (20%) compared with the overlap for birds found in interior grasslands (45%) and lagoons (55%). The greater distance traveled to roost sites by birds foraging in the foredune habitat appeared to be related to increased exposure in that habitat type. Savannah Sparrows selected foraging areas with less vegetative biomass and more bare ground than random sites. Roost sites had greater total (live) cover than foraging and random sites. Savannah Sparrows foraged alone or in loose aggregations with conspecifics. Birds roosted alone or in aggregations of up to 30 individuals. Savannah Sparrows often roost outside of their foraging areas; this study draws attention to differences in space use for roosting and foraging Savannah Sparrows. Although Savannah Sparrows maintained relatively small home ranges, they occasionally moved at larger spatial scales, suggesting a need for intact grassland patches much larger than the average home-range size. Received 18 February 2004, accepted 6 December 2004.

The relationship among foraging- and roost-site selection, behavior, and home-range size is not well understood for non-breeding emberizid sparrows. This is related, in part, to the small size, cryptic coloration, and nomadic nature of some members of this group. The degree of nomadic behavior varies among species and possibly within and among regions (Gordon 2000). In Arizona, where seed abundance can vary substantially among patches and winters, Gordon (2000) found that four species of emberizid sparrows all tended to occupy fixed home ranges during the winter period, with the Savannah Sparrow (*Passerculus sandwichensis*) exhibiting the greatest variation in movement patterns. Gordon (2000) found that local movement patterns of Savannah Sparrows differed between study sites.

There is little evidence of Savannah Sparrow fidelity to wintering grounds, and movement patterns appear to be variable (Odum

and Hight 1957, Wheelwright and Rising 1993, Gordon 2000, Ginter 2004). Understanding factors that contribute to variation in the extent of this sparrow's movements is important for its management and conservation on wintering grounds. Using flush-netting techniques, Odum and Hight (1957) found that winter home-range sizes in Georgia varied from 6 to 60 ha. Gordon (2000) did not estimate home-range sizes, but found that Savannah Sparrows in southeastern Arizona tended to remain within a fixed home range and moved an average distance of 186 m between consecutive locations. Using flush-netting, Gordon (2000) detected sedentary behavior at one site and high mobility at another. Intraspecific differences in behavior may result in variation in response to capture using flush-netting (Gordon 2000, Ginter 2004). Radio-telemetry may provide a better estimate of movement patterns and the degree of sedentary behavior.

Variation in movement patterns may be related to the distribution of seed resources across the landscape, predator avoidance, or the distribution of suitable foraging and roosting habitat. Other studies have found winter sparrow abundance to be correlated with seed

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production, suggesting that sparrows track resource abundance (Pulliam and Parker 1979, Grzybowski 1982). Unlike more sedentary grassland sparrows, such as Grasshopper (*Ammodramus savannarum*), Baird's (*A. bairdii*), Henslow's (*A. henslowii*), and Cassin's sparrows (*Aimophila cassinii*) that forage within dense grass cover (Pulliam and Mills 1977, Plentovich et al. 1999, Gordon 2000, Carrie et al. 2002), Savannah Sparrows have been observed to forage in open areas with little cover (Grzybowski 1982, Lima 1990, Lima and Valone 1991). Lima and Valone (1991) suggest that predator avoidance is an important aspect of foraging-site selection for grassland sparrows. Through experimental manipulation, they found that the availability of cover changes the composition of the winter avian community. Savannah Sparrows seem to forage within a matrix of open areas and denser cover (Watts 1991). Although little is known of Savannah Sparrow roost-site selection, most avian species are thought to select winter roost sites with greater vegetative cover due to enhanced microclimate and predator protection (Walsberg and King 1980, Buttemer 1985). We hypothesized that Savannah Sparrow foraging and roosting habitats would differ, and that the distribution of these habitats would contribute to variation in movement patterns. Movement patterns may also be related to seed abundance and we predicted that home-range size would be inversely correlated with seed abundance and biomass.

#### METHODS

*Study area.*—We conducted our study along the Texas coast on Padre Island National Seashore. North Padre Island is a long, narrow barrier island approximately 120 × 4 km (Wiese and White 1980), and is characterized by strong, moisture-laden gulf winds (Drawe et al. 1981). Winter temperatures rarely drop below freezing (Drawe and Kattner 1978). Unlike other coastal barrier islands in the Gulf of Mexico, Padre Island has a distinct grassland component; woody vegetation accounts for less than 0.2% of the plant community (Negrete et al. 1999). The interior grasslands are dominated by little bluestem (*Schizachyrium scoparium littorale*), gulf dune paspalum (*Paspalum monostachyum*), and bushy bluestem (*Andropogon glomeratus*). Upland dune

habitats are characterized by sea oats (*Uniola paniculata*), beach morning-glory (*Ipomoea imperati*), and partridge pea (*Chamaecrista fasciculata*). Dominant plants found in and adjacent to freshwater marshes are gulf cordgrass (*Spartina patens*), bulrush (*Scirpus pungens*), and spikerush (*Eleocharis flavescens*). Primary plants in saltwater marshes are halophytic, including shoregrass (*Monanthochloë littoralis*), saltgrass (*Distichlis spicata*), glasswort (*Salicornia bigelovii*), beachwort (*Batis maritima*), and sea-ox-eye (*Borrchia frutescens*) (Hatch et al. 1999).

*Radio telemetry.*—We captured birds in mist nets at 7 sites in 2002 and 11 sites in 2003 across the northern 32- × 4-km section of the island. Radio transmitters were placed on 57 Savannah Sparrows during January and February of 2002 and 2003 (21 in 2002 and 36 in 2003). We fitted birds with 0.72-g BD-2 transmitters (Holohil Systems, Ontario, Canada; 4.0–4.5% of body weight; mean life span = 26.6 days ± 0.9 SE, range = 21–37 days). We attached transmitters using the leg-back harness technique (Rappole and Tipton 1991). Harness fit was evaluated for each bird prior to release by placing the bird in an enclosure and observing its movements. If a bird's movements were restricted, the transmitter was removed and the bird was released (C. E. Gordon pers. comm.).

Initially, we attempted collecting data at a minimum of four foraging and three roosting locations per week for each bird; however, in 2003 we increased the number of locations because our 2002 data were insufficient for analyzing home-range sizes of most birds. Data on foraging locations were collected between 07:00 and 17:00 CST, whereas data on roost-site selection were collected between 20:00 and 05:00. We located most birds visually. If a bird appeared to respond to the observer's presence before being observed, we used the strength of the radio signal to mark its initial position (Vega Rivera et al. 2003). For each radio-tagged Savannah Sparrow, we recorded whether it was solitary or found in a flock, and we recorded whether the flocks were single- or mixed-species flocks. We did not record the number of individuals within flocks due to difficulty in determining flock membership. Roosting Savannah Sparrows remained stationary when approached and we

tried to avoid flushing them. If we flushed a radio-tagged sparrow from its roost site, we recorded the number of individuals in close proximity (within a 2-m radius) to the radio-tagged bird. All locations where birds were first observed were marked in UTM coordinates with handheld Garmin GPS units.

We examined Savannah Sparrow use of three distinct habitat types within specific geographic areas on the island: (1) foredunes, which separate the beach front from the interior habitats; (2) interior grasslands; and (3) the edge of the lagoon (Laguna Madre). We classified radio-tagged Savannah Sparrows by habitat type and calculated foraging and roosting areas for each habitat. We calculated the distance from the center of the bird's estimated foraging area to each nocturnal roost location to determine the mean distance traveled between foraging and roost sites. We also calculated the percentage of the roosting home range that overlapped with the foraging area.

*Habitat measurements.*—Over the two winters, we measured the structural characteristics of the vegetation at five randomly selected foraging locations per bird ( $n = 46$  Savannah Sparrows), five roosting locations per bird ( $n = 44$  Savannah Sparrows), and at paired random points. Random locations were selected by choosing a random azimuth ( $0\text{--}360^\circ$ ) and a random distance between 0 and 50 m; we used the foraging and roosting locations as center points and the algorithm suggested by Skalski (1987) to correct for bias when sampling in circular plots. A visual obstruction reading (VOR, an index of vegetation biomass), was taken using a Robel pole at each location with four readings per point (Robel et al. 1970). A Daubenmire frame ( $20 \times 50$  cm) was used to estimate percent grass, forb, litter, woody, and total (all live vegetation) cover and bare ground (Daubenmire 1959). We measured maximum height of grass and forbs (the tallest plant in each frame) and the depth of horizontal vegetation within the Daubenmire frame (Desmond 2004).

In 2003, we quantified seed abundance and biomass by collecting surface soil samples at 10 foraging locations and 10 randomly selected paired points for nine Savannah Sparrows selected randomly from our radio-tagged birds. Random points were selected using the same criteria outlined above. We collected

four subsamples at each location and each random point. The four subsamples were chosen randomly from within a 1-m radius. We placed an 8.6-cm-diameter metal hoop on the ground and scooped the soil from inside the hoop to a depth of 0.8 cm for a total of  $46.4 \times 4 \text{ cm}^3$  of soil per sample. This technique is a modification of the method used by Grzybowski (1982). Samples were placed in labeled bags and dried at  $50^\circ \text{C}$  for approximately 24–48 hr.

To analyze seed samples, a hydropneumatic root elutriator was used to separate inorganic from organic material (Gross and Renner 1989). Seeds were separated from the remaining organic material using tweezers and a  $10\times$  magnification microscope (Pulliam and Brand 1975). Seeds were identified to genus, and, when possible, to species. For each sample, seeds were counted and weighed to the nearest one-thousandth of a gram. Seeds  $>5$  mm in length or width were not included in the analyses.

*Data analyses.*—We used a non-parametric Kernel Home Range (KHR) estimator to determine the size of the home range for each bird; the KHR estimates the minimum area in which a Savannah Sparrow had a specific probability of being located (Worton 1995, Seaman and Powell 1996). We calculated a fixed KHR at 50% (core area) and 95%, and calculated smoothing parameters using least squares cross-validation (Seaman and Powell 1996, Hooe and Eichenlaub 1997). Cross-validated fixed-kernel home ranges have been found to be the most accurate of the home-range estimators (Seaman and Powell 1996). We used the ANIMAL MOVEMENTS extension program for ArcView 3.2 to perform calculations of the 50% and 95% KHR estimates (Hooe and Eichenlaub 1997). KHR estimates were calculated separately for foraging and roosting locations, and all locations combined (combined home range). Consecutive locations for individual sparrows were separated by a minimum of 12 hr and we used only those birds for which we had  $\geq 20$  telemetry locations. This resulted in  $\geq 20$  locations for foraging areas and combined home-range sizes but fewer (mean = 13) for roosting areas. However, the standard errors for foraging- and roosting-area estimates were similar and we believe the data provided a good estimate of

TABLE 1. Mean and range (ha) of winter home-range size, foraging area, roosting area, and core foraging area, and number of telemetry locations (SE) for Savannah Sparrows ( $n = 28$ ) on Padre Island National Seashore, Texas, during January and February, 2002 and 2003. Home ranges and foraging and roosting areas were calculated using a 95% Kernel Home Range (KHR) estimator; a 50% core estimator was used for core foraging areas.

Area estimated	Size (SE)	Range in area	No. telemetry locations
95% KHR			
Home range	9.1 (1.8)	0.2–31.7	35 (1.8)
Foraging area	5.6 (0.8)	1.0–19.8	22 (1.2)
Roosting area	6.6 (1.0)	0.4–17.9	13 (0.8)
50% KHR			
Core foraging area	0.9 (0.2)	0.9–4.1	22 (1.2)

roosting patterns (Table 1). Each bird was followed until the transmitter battery died, the bird lost its transmitter, the signal disappeared, or there was a confirmed mortality.

A Kruskal-Wallis test was used to examine, by habitat type, size differences in foraging areas, roosting areas, and home-ranges. We also compared mean distance traveled between foraging and roosting sites and tested for differences in percentage overlap between roosting and foraging areas among the three habitat types. For all Kruskal-Wallis tests we report the exact chi-square. All statistical analyses were performed using SAS 8.02 (SAS Institute, Inc. 1990).

Vegetation associations were evaluated by comparing foraging and roosting locations with each other and with paired randomly selected points; we used paired *t*-tests to analyze these data. We performed Shapiro-Wilkes tests to determine whether variables were normally distributed. When appropriate, we transformed data using a square-root transformation. To adjust for significance when performing multiple tests, we used the sequential Bonferroni correction (Rice 1989). We used Spearman rank correlation to test for a relationship between seed abundance and size of the 95% foraging KHR. Home-range sizes and vegetation characteristics are reported as means  $\pm$  SE.

## RESULTS

Of 57 Savannah Sparrows fitted with transmitters, we had a sufficient number of locations to calculate home-range size for 28 birds. With the exception of four birds discussed below, the birds excluded from analyses were those that died, slipped their trans-

mitters, or for which we had insufficient data (in 2002). There were three confirmed mortalities in 2002 and five in 2003. Because we detected no differences in between-year home-range sizes, we combined data from the two winters. The mean home-range size (95% KHR) was 9.1 ha and mean foraging and roosting areas were 5.6 and 6.6 ha, respectively; the mean core foraging area (50% KHR) was 0.9 ha (Table 1). We had difficulty locating four birds: two disappeared and two exhibited large-scale movement. One sparrow moved to a site approximately 2 km from its point of capture, where it remained for 5 days before returning and then permanently disappearing. A second bird moved 800 m from its point of capture, where it remained until it lost its transmitter 6 days later. Each radio-tagged sparrow foraged within a flock on at least one occasion. When foraging in flocks, Savannah Sparrows always foraged with conspecifics in loose aggregations (birds 1–10 m apart but apparently in vocal communication). We observed a mean of  $1.3 \pm 0.4$  ( $n = 43$ ) sparrows roosting within approximately 2 m of radio-tagged Savannah Sparrows. Although we suspect that radio-tagged Savannah Sparrows were roosting only with conspecifics, this could not be confirmed due to the difficulty of identifying them at night.

There were no detectable differences in sizes of foraging and roosting areas among birds using foredune, lagoon, and interior habitats ( $\chi^2_{\text{foraging}} = 1.38$ ,  $df = 2$ ,  $P = 0.50$ ;  $\chi^2_{\text{roosting}} = 5.15$ ,  $df = 2$ ,  $P = 0.081$ ; Table 2). Home-range size did differ among the three habitat types ( $\chi^2 = 8.73$ ,  $df = 2$ ,  $P = 0.010$ ; Table 2); mean home-range size of sparrows using the foredune habitat was larger than that of

TABLE 2. Kernel Home Range (95%) size (SE) for Savannah Sparrows, by habitat type, on Padre Island National Seashore, Texas, during January and February, 2002 and 2003. Different letters within columns denote significant between-habitat differences (Kruskal-Wallis test:  $P \leq 0.05$ ).

Habitat (n)	Home range (ha)	No. locations	Foraging area (ha)	No. locations	Roosting area (ha)	No. locations
Foredune (7)	16.6 (3.3) A	34.0 (4.5)	5.7 (1.3) A	21.9 (3.1)	9.9 (1.4) A	12.1 (1.5)
Grassland (13)	7.0 (1.6) B	33.2 (2.5)	6.1 (1.0) A	20.8 (1.5)	10.0 (4.6) A	12.4 (1.1)
Laguna Madre (8)	5.9 (1.7) B	41.2 (3.6)	4.4 (1.0) A	25.0 (2.0)	5.7 (1.8) A	16.2 (1.7)

sparrows using the other two habitat types. The mean distance traveled between the center of the estimated foraging areas and roosting locations differed among the three habitat types ( $\chi^2 = 10.29$ ,  $df = 2$ ,  $P = 0.026$ ). Sparrows using foredune habitat traveled farther between the centers of their foraging areas and roosting locations (mean = 337 m) than birds using interior grasslands (mean = 108 m) or lagoons (mean = 107 m). The percentage of overlap between roosting and foraging areas differed among the three habitat types ( $\chi^2 = 7.43$ ,  $df = 2$ ,  $P = 0.020$ ). Overlap for sparrows using foredune habitat was minimal (20%), whereas it was 45 and 55% for birds using interior grassland or lagoon habitats, respectively (Fig. 1). For example, there was no overlap of roosting and foraging areas for bird #279, but some birds using interior grassland and lagoon habitats had roosting areas completely contained within the foraging area (#840) or vice versa (#71); others had some overlap, but also maintained distinct foraging and roosting areas (#959).

Foraging areas had more bare ground and less VOR and horizontal depth than randomly selected points. When compared with roosting sites, foraging sites had more bare ground, less total cover, and lower horizontal depth. Roost sites had greater total cover and grass cover than randomly selected sites (Table 3).

Seed biomass did not differ between foraging and random sites and was positively correlated with the size of the 95% foraging KHR (Spearman rank correlation:  $r = 0.68$ ,  $P = 0.042$ ). On the other hand, seed abundance was significantly greater in samples collected at foraging sites compared with random sites (Wilcoxon-Mann-Whitney  $U$ -test = 62.5,  $P = 0.043$ ). There was no relationship between seed abundance at foraging sites and size of the 95% foraging KHR (Spearman rank correlation:  $r = 0.28$ ,  $P = 0.46$ ). Seed biomass

and abundance included seeds of all shapes and sizes that could be reasonably consumed by Savannah Sparrows; seeds  $>5$  mm in width or diameter were excluded from the analyses. The most common seed species were present at both foraging and random locations and included little bluestem, *Cyperus* spp., *Eleocharis* spp., camphorweed (*Heterotheca subaxillaris*), *Dichanthelium* spp., *Paspalum* spp., fall witchgrass (*Digitaria cognata*), and panicgrass (*Panicum amarum*).

## DISCUSSION

Savannah Sparrows exhibited strong sedentary behavior within winters; the majority of their foraging movements were restricted to an average core area of approximately 1 ha. The scale of movement detected in this study was smaller than previously estimated. However, we did observe extremes in home-range size ranging from 0.15 to 31.7 ha. We also observed large-scale movements of two Savannah Sparrows not included in the home-range analyses, with one moving as far as 2 km from its point of capture. Two radio-tagged sparrows disappeared altogether from the study area. Using a flush-netting technique, Gordon (2000) recaptured 3.8% (within winters) of the Savannah Sparrows banded on 7-ha plots, but had much higher recapture rates for Baird's, Grasshopper, Vesper (*Pooecetes gramineus*), and Cassin's sparrows. The low recapture rate for Savannah Sparrows in Arizona may indicate that the average winter home-range size is larger there than it is in coastal south Texas, or it may indicate that radio telemetry is a more reliable method for estimating home-range size and the degree of sedentary behavior for this species. Our study is the first to use radio telemetry to estimate winter home-range size for Savannah Sparrows. The small, average home-range size in south Texas may indicate a reliable resource

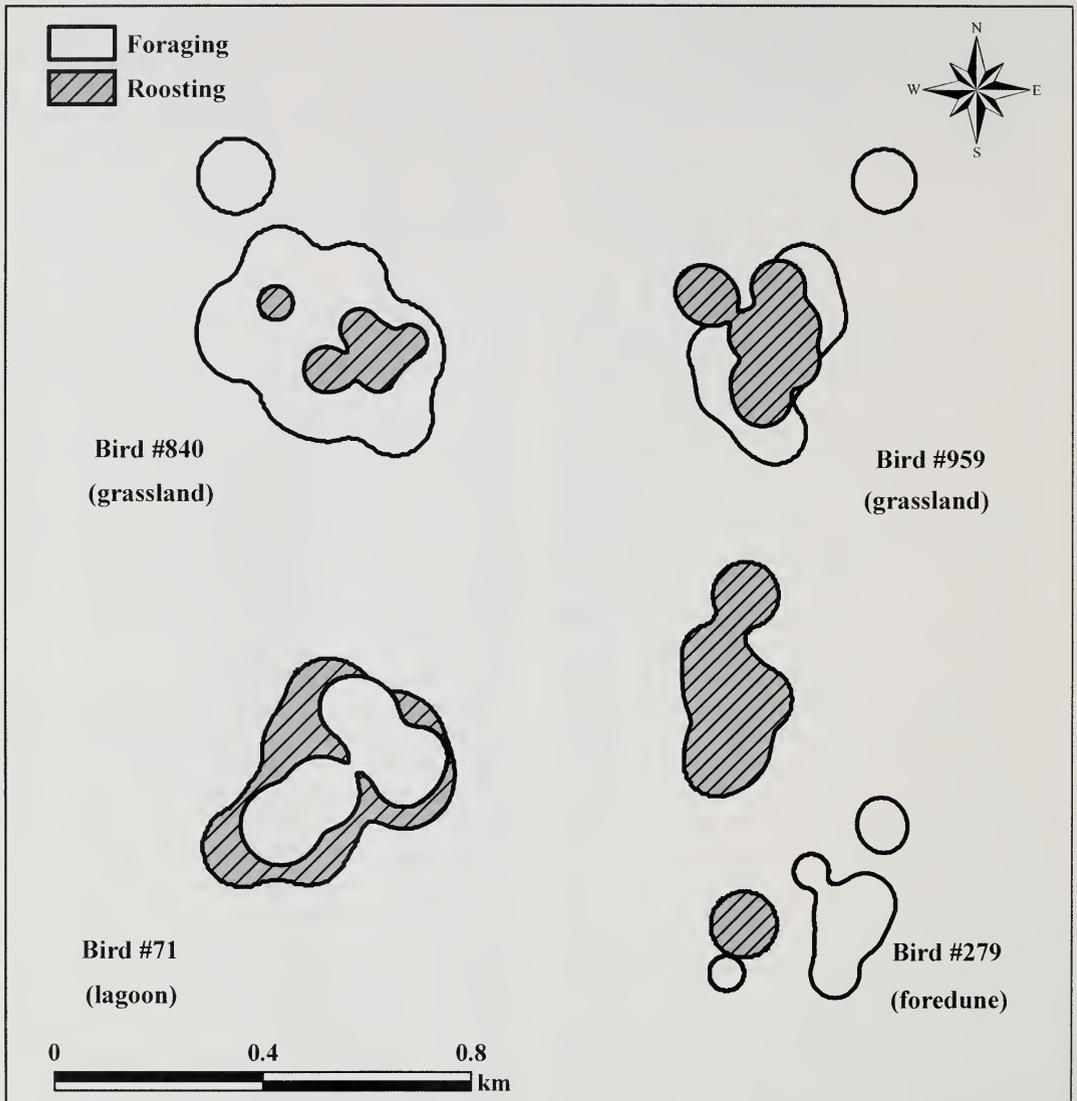


FIG. 1. Examples of distribution of foraging and roosting areas within home ranges of four Savannah Sparrows wintering on Padre Island National Seashore, Texas, January and February, 2002 and 2003. The roosting area of bird #840 (interior grasslands habitat) was 100% contained within its foraging area; 71% of the roosting area of bird #959 (interior grasslands habitat) was contained within its foraging area; 100% of the foraging area of bird #71 fell within its roosting area. There was no overlap between roosting and foraging areas of bird #279 (foredune habitat).

base to maintain sparrows within a small area throughout the winter period. Alternatively, Savannah Sparrows may tend to occupy relatively small areas (1 ha) for short periods of time (1–2 months), but may occasionally wander at larger spatial scales during the course of the winter (November–March). This could explain the large-scale movement we ob-

served for two sparrows in this study, and the high degree of variability in recapture rates between sites in Arizona (Gordon 2000).

Movement patterns between roosting and foraging sites have not been previously reported for wintering Savannah Sparrows. The mean distance moved from the center of foraging areas to roosting sites was 165 m, with

TABLE 3. Comparisons of mean vegetative structure at foraging, random, and roosting areas within Savannah Sparrow home ranges during January and February, 2002 and 2003 on Padre Island National Seashore, Texas. Asterisks denote significant differences (paired *t*-test:  $P \leq 0.05$ ) between paired locations.

Variable	Foraging versus random areas (SE)		Roosting versus random areas (SE)		Foraging versus roosting areas (SE)	
	Foraging	Random	Roosting	Random	Foraging	Roosting
% Grass	66.2 (3.3)	59.1 (3.0)	76.9 (3.3)*	62.7 (3.4)*	68.9 (3.3)	69.0 (3.7)
% Forb	24.9 (3.0)	32.1 (2.8)	21.6 (3.3)	25.2 (2.5)	22.8 (3.0)	27.7 (3.7)
% Bare ground	41.7 (2.2)*	31.2 (2.1)*	30.6 (2.5)	35.8 (2.7)	41.8 (2.2)*	32.2 (2.2)*
% Leaf litter	8.1 (1.7)	7.4 (1.7)	4.1 (0.7)	8.5 (2.0)	7.7 (1.7)	6.0 (1.2)
% Total cover <sup>a</sup>	50.8 (2.0)	58.5 (2.4)	65.3 (2.2)*	53.8 (2.9)*	50.6 (2.0)*	61.8 (2.5)*
Vegetation biomass <sup>b</sup>	1.1 (0.1)*	1.5 (0.1)*	1.3 (0.1)	1.4 (0.1)	1.1 (0.1)	1.3 (0.1)
Horizontal depth (cm)	3.6 (0.5)*	6.8 (0.8)*	5.7 (0.6)	5.1 (0.7)	3.7 (0.5)*	5.4 (0.5)*
Maximum grass height (cm)	25.5 (1.7)	31.6 (1.9)	33.2 (1.8)	34.4 (2.4)	26.6 (1.7)	28.3 (1.5)

<sup>a</sup> Total cover (grass, forb, woody).

<sup>b</sup> Vegetation biomass as indexed by visual obstruction readings (Robel et al. 1970).

some individuals traveling 400–600 m. Birds foraging along the foredunes (nearest to the ocean) always moved inland to roost and traveled the greatest distance to roosting sites; there was little overlap between roosting and foraging areas of these birds. The home-range configuration of sparrow #279 illustrates the separation of foraging and roosting locations used by birds in foredune habitat (Fig. 1). Foredues, which sometimes extend no farther inland from the ocean than 100 m, are subject to the harshest environmental conditions on the island. Movement inland by roosting Savannah Sparrows is likely an attempt to escape exposure to the persistent winds coming off the Gulf of Mexico and to find appropriate roosting microhabitat.

Savannah Sparrows, the dominant winter sparrows on the island, foraged in open areas either as solitary individuals or as members of loosely spaced aggregations of conspecifics. Open areas likely provide easier access to available resources. These birds also foraged in areas with higher seed abundance than randomly selected locations, suggesting that they may cue in on resource abundance. Grzybowski (1982, 1983) also found individual and loose aggregations of Savannah Sparrows foraging in areas with low vegetation height and density. Although he did not examine Savannah Sparrows specifically, he found a positive relationship between avian density and seed abundance. Variation in the abundance of wintering emberizid sparrows has been linked to seed production in southeastern Arizona (Pulliam and Brand 1975, Dunning and

Brown 1982). We predicted that foraging areas would be smaller where abundance and biomass of seeds were greater. The lack of a negative relationship suggests that factors other than seed abundance—such as proximity to the coast, the distribution of suitable foraging and roosting patches, or predator avoidance— influence winter home-range size and may also influence the variation observed in Savannah Sparrow movements. The small sample size (nine birds) also may have contributed to the lack of an observed relationship.

Savannah Sparrows foraged in open areas within a matrix of open areas and denser vegetation. This was evident from the greater vegetative biomass at random points compared with that of foraging sites within individual home ranges. Other studies report that wintering Savannah Sparrows forage in open areas adjacent to cover, and suggest that nearby vegetative cover may offer protection from predators (Pulliam and Mills 1977, Watts 1991). This has also been reported for other wintering sparrow species (Lima 1990, Lima and Valone 1991). The foredune habitat used by some sparrows on Padre Island is especially patchy, and may be attractive as foraging habitat, despite the longer distances between foredunes and roosting sites.

Savannah Sparrow roosting sites were often interspersed within or around foraging locations (Fig. 1), and they had greater total cover than foraging and random sites. Greater horizontal vegetation depth at roost sites may be important because it provides space for birds to roost and move under the vegetation with-

out being exposed. Although temperatures rarely dip below freezing in south Texas, frequent winter storms and winds coming off the Gulf Coast likely affect the energy expenditure of roosting individuals. As a result, sparrows roost in areas that provide greater protection from climatic factors, and individuals foraging close to the coast travel farther inland to roost. Other studies of roost-site selection suggest that individuals select sites with the greatest microclimate protection (Kendeigh 1960, Gottfried and Franks 1975, Gyllin et al. 1976, Buttemer 1985). Greater cover could serve to reduce predation risk and provide increased protection from exposure, thus reducing overnight energy expenditure (Walsberg and King 1980). We were able to approach roosting Savannah Sparrows within 1 m, but we were unable to determine the exact proximity of individuals roosting in aggregations. It was apparent, however, that some individuals roosted close together. The mean number of birds roosting in close proximity to each other was low (<5 sparrows), but variation was high. We sometimes observed as many as 30 sparrows roosting in close proximity, suggesting that Savannah Sparrows may derive a benefit from communal roosting, such as reduced predation risk or energy conservation. Other avian species also roost in aggregations during the winter months (Walsberg 1990, Heinrich 2003). With the exception of studies on species that form large communal roosts, studies of nonbreeding passerines have generally disregarded roosting behavior and roost-site selection, often with the assumption that diurnal movement patterns encompass the roosting areas. Our study shows that the distribution of foraging and roosting habitat influences movement patterns and overall home-range size; Savannah Sparrows often roost outside of their foraging areas, and they have specific habitat requirements for foraging and roosting locations.

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## BREEDING ECOLOGY OF THE PUAIOHI (*MYADESTES PALMERI*)

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**ABSTRACT.**—We studied the breeding ecology of the critically endangered Puaiohi (*Myadestes palmeri*), a poorly known Hawaiian thrush endemic to the island of Kauai. From 1996 through 1998, we monitored 96 active nests over the course of three breeding seasons. Mean clutch size was 2.0, and pairs produced an average of 1.5 fledglings/successful nest. Pairs re-nested after failure and some raised multiple broods. The mean annual reproductive effort was 2.1 nesting attempts/territory, and pairs produced a mean 1.1 fledglings/attempt. Large differences in nesting effort and productivity occurred among years, with mean number of fledglings/territory ranging from 0.4 to 4.9. Predation by owls (probably Short-eared Owls, *Asio flammeus*) and introduced rats (probably black rats, *Rattus rattus*) accounted for most nest failures. The presence of non-breeding floaters in the population and their largely unsuccessful attempts to gain territories in the study area suggest that the population is near carrying capacity. The high reproductive potential of the Puaiohi may help explain its persistence despite the species' historical rarity. Received 29 April 2004, accepted 22 November 2004.

The Puaiohi (*Myadestes palmeri*) is a rare and poorly known thrush restricted to forests above 1,000 m elevation on the island of Kauai in the Hawaiian Islands. Of the five Hawaiian thrushes, it is the most divergent vocally, morphologically, and behaviorally (Pratt 1982). Except for the Omao (*M. obscurus*) on the island of Hawaii, the other species are considered critically endangered or extinct (Collar et al. 1994, Reynolds and Snetsinger 2001).

Intensive efforts over the last 4 decades to document the status of Hawaii's forest birds suggested that the Puaiohi was exceedingly rare and had experienced a range contraction since the 1960s (Sincock et al. 1984, Scott et al. 1986, Pyle 1994). In the course of these studies, a number of factors were implicated in the loss of Hawaii's forest bird populations. It is thought that habitat modification, avian disease, competition, and predation have acted in concert to diminish available habitat and

reduce survival and reproduction. Surveys conducted by the U.S. Fish and Wildlife Service (USFWS) and Hawaii Department of Land and Natural Resources (DLNR) in 1993 and 1994 suggested that the Puaiohi was on the brink of extinction (USFWS, DLNR unpubl. data).

Published descriptions of three known Puaiohi nests suggest that the Puaiohi usually nests on cliffs along streambeds (Kepler and Kepler 1983, Ashman et al. 1984, Harry et al. 1995). These descriptions, along with a few incidental observations and a sparse record of published anecdotal information (Perkins 1903, Richardson and Bowles 1964), were all that was known of the breeding biology and life history of the Puaiohi. The discovery in April 1995 of a fledgling Puaiohi and at least three breeding pairs on the Alakai Plateau of Kauai, near the Koaie Stream Gauging Station (Harry et al. 1995), prompted a 3-year interagency study. The goals of the study were to determine the status of the population, collect life-history information, assess limiting factors, and develop and evaluate management strategies to promote the protection and expansion of this species into appropriate habitat within its historical range. Concurrently, the Zoological Society of San Diego (ZSSD) and U.S. Geological Survey (USGS) developed captive propagation and release techniques for the closely related Omao to assist in expanding the range of the Hawaiian *Myadestes* (Kuehler et al. 2000, 2001; Fancy et al. 2001).

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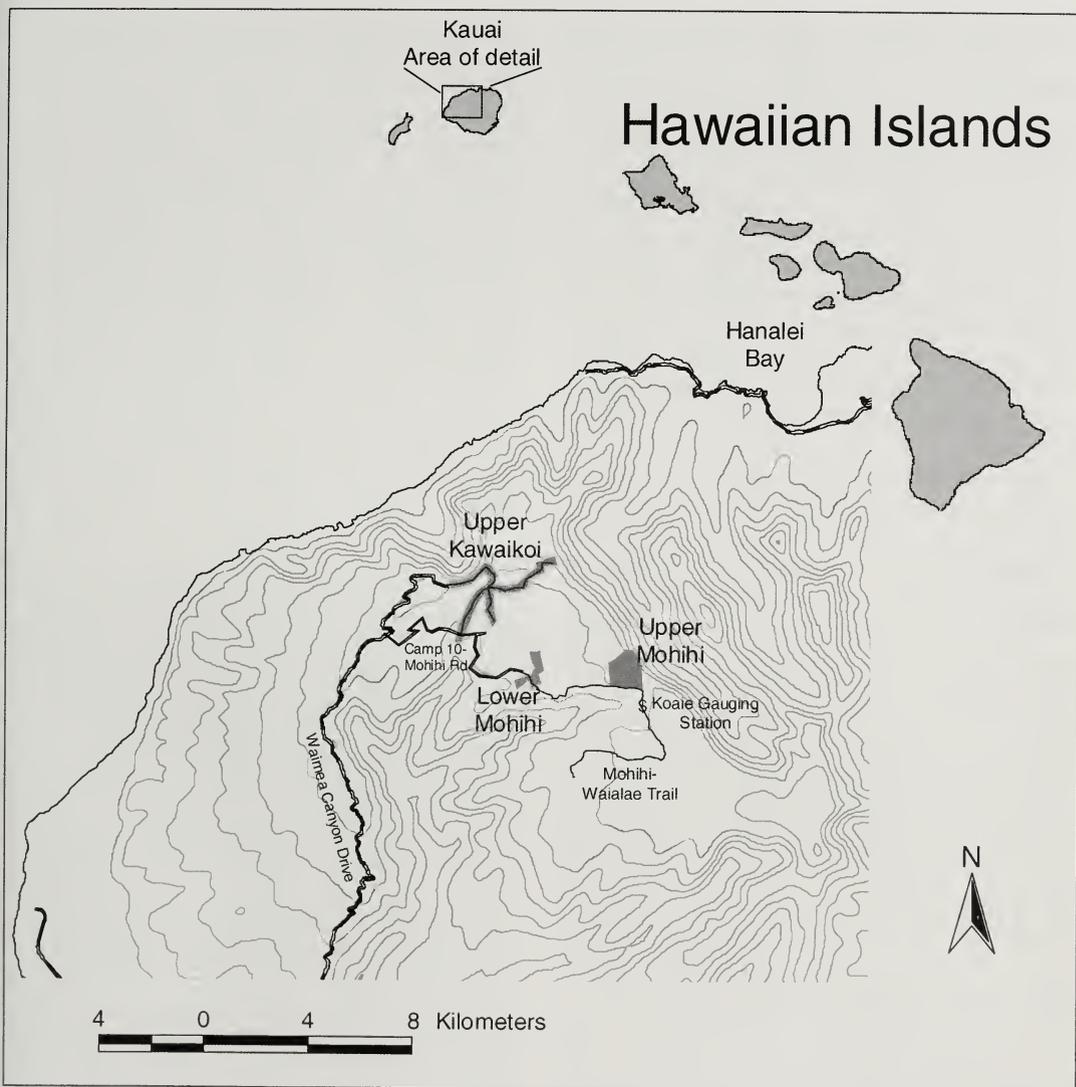


FIG. 1. Upper Mohihi, lower Mohihi, and upper Kawaikoi Puaiohi study areas (shaded) on the island of Kauai (1995–1998). Contours are 150 m apart.

## METHODS

*Study area.*—We established a base camp at the Koae Gauging Station at the 4.0-mile (6.5 km) marker along the Mohihi-Waialae Trail (Fig. 1) due to its proximity to previously noted Puaiohi breeding activity. During September 1995–January 1996, we conducted preliminary surveys in this area and other areas of suitable habitat. We monitored these areas from 1996 through 1998. Through our initial surveys we located a population concentration at 1,250 m elevation along the upper stretches of the Mohihi Stream and its tributaries, and

we selected a 2-km<sup>2</sup> study area that included 66 ha along 3.8 km of the Mohihi Stream bottom. We also found several isolated Puaiohi pairs in the neighboring Koae drainage and monitored their breeding activity as well. Lastly, we selected 4 km of stream bottom on the lower Mohihi Stream (where Puaiohi were rare) and 8 km of stream bottom and trails in the upper Kawaikoi Stream drainage (where Puaiohi were not detected) to conduct Puaiohi surveys and habitat-related research.

The vegetation at each of the three study areas (upper Mohihi and territories in the ad-

jacent Koaie drainage, lower Mohihi, and upper Kawaikoi) was dominated by a dense ohia (*Metrosideros polymorpha*) canopy. A wide variety of other trees and shrubs made the forest structurally diverse with a dense, well-developed understory. The rainy season extended from November through March and was wet but variable, with an average daily rainfall of 19.2 mm/day for 1995–1996 and 1996–1997. The mean daily rainfall for the same period in 1997–1998 was just 6.5 mm/day. The upper Mohihi differed from both the lower Mohihi and upper Kawaikoi in having narrower, steeper drainages with more vertical cliff walls.

*Nest monitoring.*—We searched for nests at known activity centers at least once every 3 days from the onset of breeding in March through the end of breeding in September (August in 1998). Weather permitting, we checked nests every other day and recorded the status: inactive (under construction, fledged, failed, or in latency—the lag between nest completion and the first egg), laying, incubating, hatching, nestling, or unknown. We counted nestlings and/or eggs when this could be done without undue disturbance to the nest. Using a combination of clues, we attempted to determine the cause of nest failures. We attributed predation to owls if the nest was completely removed and if we had observed owl activity nearby prior to predation. If we found partially eaten remains of young or adults or the presence of rat feces in the nest, we concluded that rat predation was the cause of nest failure. For each year we report the mean  $\pm$  SD for the various stages of nesting and the length of the breeding season (annual period from mean first egg laid date through mean final nest failure or fledge date), which was determined for pairs in which all breeding activity was documented within a year.

Every 1–3 days we monitored selected ( $n = 43$ ) nests for 1–4 hr during all stages of nesting to determine nest attendance rates and nestling food requirements. We monitored activity with a spotting scope or binoculars from a blind (15–50 m from the nest) or, if blind placement was not possible, from a sufficient distance so as not to influence normal behavior. Observers recorded all nest activity (sex and age of the attending bird, behavior, time, and weather conditions) by dictating into a

micro-cassette recorder. When a bird was not identifiable by the presence of a unique breast pattern of retained juvenile feathers or color bands, age was determined by the presence or absence of retained juvenile scalloping. Sex of unknown birds was determined by behavior (brooding and incubating were associated only with females in this study), evidence of a brood patch (females; Ashman et al. 1984, this study), or the concurrent observation of the bird's known-sex mate (e.g., the male was singing from a perch near the nest; only males sang in this study) and no evidence of helper activity at the nest. Additionally, in 1997, while adults were absent from nests, we measured and described eggs ( $n = 29$ ) and color-banded, weighed, and measured nestlings ( $n = 20$ ).

We found nearly all Puaiohi nests on shelves or in cavities of streamside cliff walls. Once nests were no longer active, we recorded wall height at the nest, nest height on the wall, cavity or shelf dimensions (maximum depth, height, width), concealment (single ground-based visual estimate of how obscured [%] the nest was from a distance of 5 m from the nest), wall vegetation, distance to flowing stream, and direction of exposure. We recorded nest material for nests in fresh condition and took the following nest measurements: overall height, depth of cup, width of rim, and diameter of cup. Nest characteristics are reported as means  $\pm$  SD. Sample sizes varied for some characteristics, as nest and cavity measurements required close inspection of the nest site and many nests were too high to allow for this. In other cases we failed to collect complete information.

*Territory size and spacing.*—The rugged terrain made it impossible to follow individual Puaiohi and map territory boundaries. However, we were able to map locations of nests and sightings of color-banded birds using compass bearings and measured distances from known points on a 1:1,000 scale map of the study area. Using plotted positions for active nests, we measured the straight-line distance to the nearest neighbor's active nest, and report the mean of this value as a measure of nest density. When an active nest was surrounded by neighboring territories that were occupied by non-nesting Puaiohi, we recorded no value.

*Management intervention.*—We removed eggs from some nests for captive propagation and poisoned rats in the vicinity of active nests to reduce rodent predation. Eggs were taken from one inactive and six active nests over the course of the study (seven eggs from three nests in 1996 and eight eggs from four nests in 1997). We distributed four tamper-resistant bait stations containing 227 g each of Eaton's Bait Block Rodenticide (contains 0.005% diphacinone) evenly on the ground below nests ( $n = 27$ ) and 5–20 m from the base of the nest cliff. Bait stations were placed only around nests that were found at least 1 week before fledging. Rats must repeatedly ingest the diphacinone bait over approximately 7 days for the bait to be effective, and recent fledglings often perch low in bushes or on the ground for a few days after leaving the nest, making them susceptible to rat predation. We checked and replaced bait weekly according to label instructions. Because protecting nests of this species was a high priority, nests were not randomly selected for bait treatment. We did not treat nests discovered within 7 days of fledging, those >20 m high, those where terrain did not allow access to the base of the nest wall, and those discovered when personnel were insufficient to maintain the bait stations.

We tested for independence of nest fate for nests that were and were not protected by rat poisoning using a chi-square test (Statistix for Windows 2.0,  $\alpha = 0.05$ ). Nest fate was categorized as failed (four categories) or fledged. The four failure categories were rat predation, owl or unknown predation, non-predation failure, and unknown.

We attempted to minimize the effects of our interventions on our data. We did not use data on nests from which eggs were removed for captive propagation in the calculation of breeding season length or fecundity statistics. In determining nest survival rates (see below), we used data only from unprotected nests. As most of the nests from which eggs were removed for captive propagation were in the middle of our study area, the effect of these artificial failures could have had unknown effects on neighboring territories. Similarly, rat control at nests may have influenced rat populations at neighboring nests where there was no rat control. Both effects are likely negli-

gible, given the Puaiohi's propensity to rapidly re-nest following nest failure and the relatively large nearest-neighbor distances between active nests.

*Reproductive effort and success.*—We used Mayfield's (1961, 1975) method to determine daily and overall survival rates for the incubation ( $n = 633$  egg-days [43 nests]), hatch ( $n = 90$  eggs [45 nests]), and nestling ( $n = 715.5$  nestling-days [41 nests]) stages for nests in the upper Mohihi study area that were not protected against rats. When nests fledged or failed between visits, fate was assigned to the midpoint between observations. We present 3-year daily survival rates for the incubation and nestling periods as mean  $\pm$  SE. Because we were uncertain of hatching period length, we treated hatching as either successful or unsuccessful and report hatching survival simply as percent eggs hatched. We calculated egg-to-fledging survival as the product of survival probabilities (incubation, hatch, and nestling).

We documented the season-long reproductive success for 48 territories over the 3 years of our study. A few individuals ( $n = 6$  birds at 12 territories) were color marked, and we could occasionally identify individuals ( $n = 13$  birds at 11 territories) through the presence of unique residual scalloping on the breast feathers in second-year (SY) birds. No color-banded individuals were observed actively breeding until 1997.

We report measures of reproductive success per territory (rather than per female). To count the number of young fledged, we visited all nests within 3 days of the fledge date and again  $\leq 1$  week later. Accurate counts were possible because (1) parents fed new fledglings often, (2) new fledglings were poor fliers, (3) they remained perched in low shrubs <50 m from the nest during the first few days after fledging, and (4) they typically stayed within 100 m of the nest during the next few weeks. We used the maximum count of observed young fledged to calculate fecundity statistics. We report annual means and 3-year means  $\pm$  SD for fledglings/territory, young fledged/successful nest, nesting attempts/territory, and fledglings/attempt. We compared fledging dates of one- and two-chick nests using ANOVA, and we compared the time from nest completion (for successful versus failed

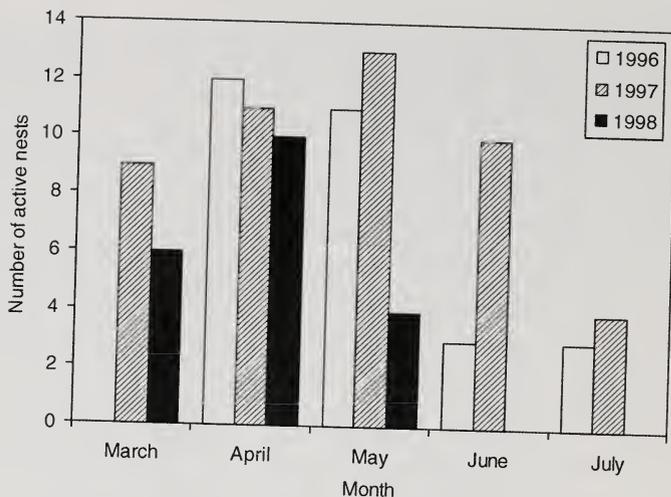


FIG. 2. Number of active Puaiohi nests ( $n = 96$ ) by month according to first egg date. We back-dated for nests found after this date ( $n = 56$ ), assuming a 13.5-day incubation period and 18.3-day nestling period (this study). Some March and April nests may have been missed in 1996 due to a lack of observer familiarity with the study area.

nests) until the onset of renesting with a  $t$ -test (Statistix for Windows 2.0,  $\alpha = 0.05$ ).

**Survival.**—As time allowed, we trapped, banded, and color marked Puaiohi using mist nets set up in the vicinity of active nests or along ridgetops where Puaiohi were regularly observed. Sample sizes were too small to use capture-recapture modeling to estimate survival, and we report minimum annual survival based on resightings for two age categories (HY, AHY) from one breeding year to the next, using April as the start of the breeding season.

## RESULTS

The Puaiohi breeding season began in March–April and usually ended in August, although in one year it continued into September. We found no active nests after August, but a recently fledged juvenile was observed in late September, indicating nesting can continue into that month. Breeding season lengths were 87 days (1996), 132 days (1997), and 51 days (1998).

The complete nesting cycle took 46 days: nest construction lasted  $2.9 \pm 2.0$  days (range = 1–7 days,  $n = 15$ ), the latency period was  $9 \pm 0.6$  days (range = 8–10 days,  $n = 12$ ), incubation lasted  $13.5 \pm 0.6$  days (range = 13–14 days,  $n = 4$ ), and the nestling period was  $18.3 \pm 1.7$  days (range = 16–22 days,  $n$

= 13). Eggs were laid one/day. Incubation began with clutch completion and hatching was synchronous (<24 hr) within broods.

**Territory occupation and nest density.**—We found 112 nests, 96 of which were active (Fig. 2). The active nests were distributed over the 3 years as follows: 1996—29 nests (representing a complete reproductive effort in 12 territories plus a partial effort in 8 territories); 1997—47 nests (representing complete reproductive effort in 14 territories plus partial effort in 10 territories); 1998—20 nests (representing complete reproductive effort in 22 territories plus partial effort in 4 territories). The remaining nests either were not used or were found after use and were distributed over the period of the study as follows: 4 nests (1996), 10 nests (1997), 2 nests (1998). In addition, we found 97 Puaiohi nests that had been constructed and possibly used in a year prior to their discovery.

Puaiohi pairs were distributed at approximately 150-m intervals along 3.8 km of the Mohihi Stream. Mean straight-line distance between active nests was  $86 \pm 17$  m (range = 59–119 m) in 1996,  $79 \pm 14$  m (range = 58–103 m) in 1997, and  $133 \pm 40$  m (range = 98–204 m) in 1998. Twenty-four territories were occupied by territorial pairs within the accessible portion of our study area throughout the study. The density of territorial Pu-

TABLE 1. Puaiohi nest and nest-site characteristics, Mohihi drainage, Alakai Swamp, Kauai, 1996–1998.

	<i>n</i>	Mean	SD	Maximum	Minimum
Height of wall (m)	157	9.5	4.8	35	3
Height above ground (m)	172	4.2	2.6	16	0.6
Distance from stream (m)	151	7.6	9.7	40	0
Width of nest cavity (cm)	46	39.4	23.4	90	7
Height of nest cavity (cm)	46	26.9	13.2	70	10
Depth of nest cavity (cm)	38	21.4	10.8	50	0
Nest concealment (%)	153	69	31.2	100	0
Outer diameter of nest (cm)	33	14.3	2.7	21	10
Inner diameter of nest (cm)	27	8.0	1.3	10	6
Height of nest (cm)	31	8.1	3.5	14	2
Nest-cup depth (cm)	27	5.4	1.5	8.7	3
Nest-rim thickness (cm)	29	3.2	0.7	4.5	2
Direction of exposure (°)	144	161	106	338	0

aiohi in the Mohihi study area was 6.3 pairs/km of primary stream bottom. The additional length of feeder streams that were too short to support more than a single territory were not included in the calculation of primary stream bottom. Non-territorial, single birds were also observed throughout the study area; however, because many of these birds were unbanded and could not be sexed accurately, we could not determine the size or structure of this population. Individual birds within a territory were occasionally replaced, but only one new territory was established in 3 years. When uniquely plumaged ( $n = 13$ ) or color-banded ( $n = 6$ ) individuals held territories, we observed only one case of turnover of a bird within a breeding season. All banded birds (two adult males and one adult female) that we monitored on breeding territories in 1997 returned to defend the same territory in the 1998 breeding season.

At least 10.0% of territories had SY females and  $\geq 6.7\%$  had SY males ( $n = 60$  pair-years). At 8.0% of 87 nests, we noted some form of helper activity in which non-breeding Puaiohi helped in the defense and maintenance of nests and/or feeding of young. These birds were fledglings from previous clutches of the same pair ( $n = 2$ ) or SY non-breeding birds with an unknown relationship to the breeding adults ( $n = 5$ ); in one case, the SY helper was known not to be related to either breeding adult.

*Nest sites, nests, and eggs.*—Most nests were constructed in cavities or on shelves of streamside cliff faces. Only 5% of active nests

( $n = 93$ ) were in other locations: four were in secondary cavities in dead ohia snags, and one was in a crevice along the side of fallen log that bridged a small stream. One inactive nest was found in the trunk of a hapuu (*Cibotium* sp.) tree fern.

Nest sites ranged from true cavities, in which the nest was completely concealed and accessed through a small hole in the cliff wall, to exposed flat shelves with little protective cover (Table 1). The majority of nests were positioned on flat shelves partially concealed from above by a protective “umbrella” of ferns and a slight overhang of the cliff nest wall. While two nest walls were dry and covered with only a light growth of lichen, 97% ( $n = 77$ ) were damp and covered with a verdant growth of small, native plants: native ferns (predominantly *Sadleria squarrosa*), liverworts, and scattered small shrubs and trees (e.g., olapa and lapalapa, *Cheirodendron* spp.; *Cyanea hirtella*; kanawao, *Broussaisia arguta*; pukiawe, *Styphelia tameiameia*; and ohelo, *Vaccinium* spp.).

Nests ( $n = 110$ ) were open-cupped with an outer matrix composed of mounded native mosses, uluhe (false staghorn fern, *Dicranopteris linearis*), liverworts, other bryophytes, painiu (a native lily, *Astelia* spp.) and sedge (*Carex* spp.) leaves, clubmosses (*Lycopodium* spp.), other ferns, grasses, and ohia rootlets. The cup lining was woven of pulu (a soft hair-like substance from hapuu), moss sporophytes, shredded grasses and sedges, or painiu leaves. Usually, an untidy mass of nesting material formed a tail, up to 20 cm long, extend-

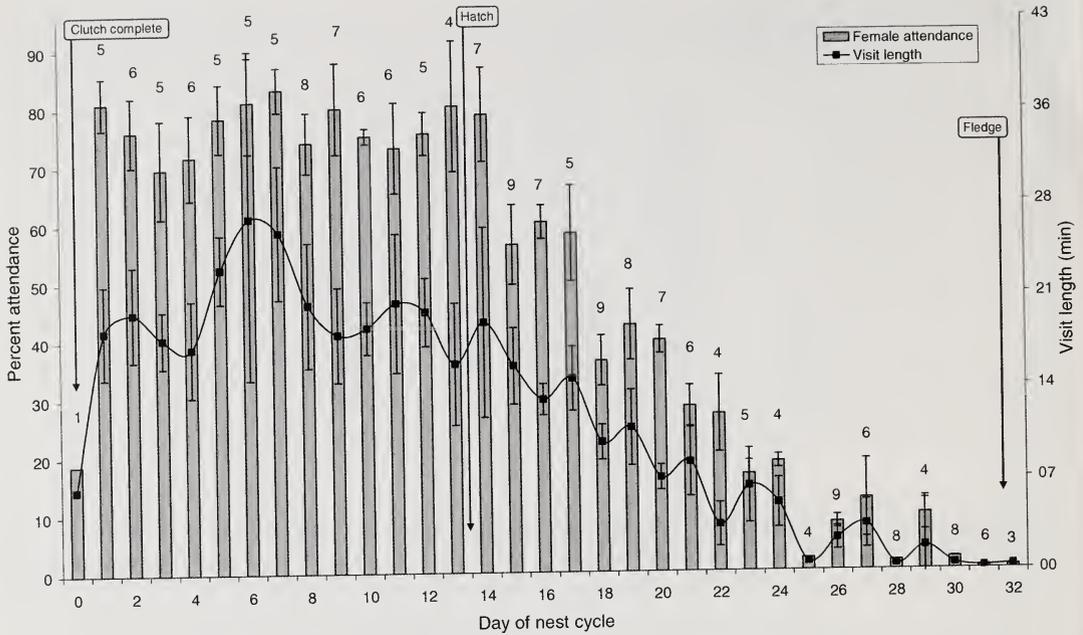


FIG. 3. Female Puaiohi nest attendance and nest-visit duration. Numbers of nests monitored are shown above bars. Error bars are  $\pm$  SE.

ing out of the cavity mouth or off the shelf ledge from the base of the nest.

All clutches consisted of 2 eggs ( $n = 39$ ). Eggs had a smooth surface and their shape varied from sub-elliptical to ovoid. Eggs ( $n = 29$ ) measured  $24.77 \pm 1.70$  mm (range = 22.11–29.80 mm)  $\times$   $18.18 \pm 1.23$  mm (range = 15.75–21.16 mm), and eggshell thickness ( $n = 3$ ) was  $0.14 \pm 0.02$  mm (range = 0.12–0.16 mm).

Background color of eggs varied, sometimes within a clutch, from a very pale greenish-blue at the light end of the spectrum to brownish-mauve at the dark end. All eggs had irregular rust, brown, mauve, and tan splotches and black and brown scrawls scattered over the surface, but concentrated at the blunt end.

*Nesting through fledgling observations.*— During incubation, the male was responsible for territory defense; after hatching, he fed the female and young. Incubation and brooding were performed solely by the female, but both adults shared provisioning and maintenance duties (females responsible for 56% of the nest visits, males 9%, and undetermined parent or helper 35%;  $n = 848$  nest visits in 461 hr of observation at 42 nests). During the nestling period, female visitation rates were  $2.8 \pm$

0.2 visits/hr. Males made  $0.68 \pm 0.08$  visits/hr during the same period.

Overall nest attendance was fairly high during incubation and then gradually dropped off as brooding proceeded (Fig. 3). Female nest attendance was  $81 \pm 4\%$  SE ( $n = 5$ ) a day after clutch completion and averaged 77% ( $n = 73$ ) during the incubation period. One day after hatch female attendance dropped to  $56 \pm 7\%$  SE ( $n = 9$ ).

Over the entire nesting period, the relative frequencies of provisioning nestlings with invertebrates and fruit were nearly equal; however, young were fed invertebrate prey exclusively until 6 days of age, when fruit was first incorporated into the nestling diet. Nestlings received fruit during 48% of the feedings in which the food item was observed ( $n = 79$ ). In order of decreasing frequency, these fruits were olapa/lapalapa, painiu, kanawao, ohelo, and “thimbleberry” (West Indian raspberry, *Rubus rosifolius*). Invertebrates were fed to nestlings 51% of the time. In order of decreasing frequency, these were moths, damselflies, earthworms, caterpillars, dragonflies, spiders, beetle larvae, and beetles. On one occasion we observed a nestling being fed a skink.

Young in one-chick nests ( $n = 4$  nests) had

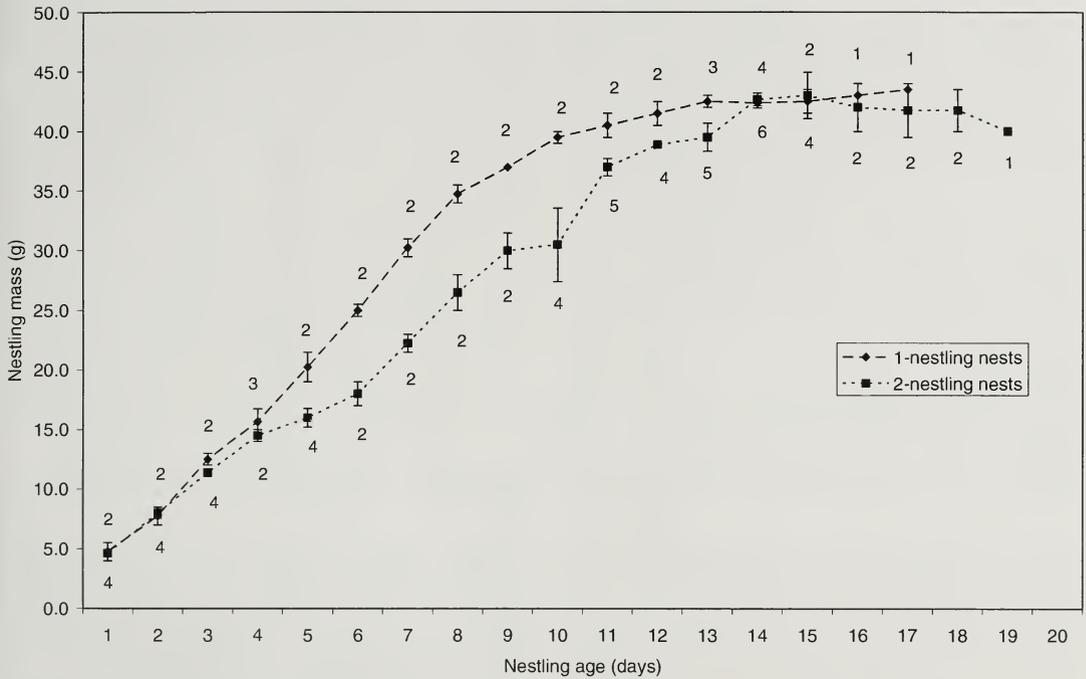


FIG. 4. Puaiohi nestling growth curves (mean mass, standard error bars). Number of nestlings weighed are shown above (1-nestling nests,  $n = 4$ ) or below (2-nestling nests,  $n = 16$ ) each point. Young in 1-nestling nests fledged at days 16–19, and, in 2-nestling nests, they fledged at days 16–21.

mean weights that were greater than those of young in two-chick nests ( $n = 16$  nests) through early development, but once the chick's growth in one-chick nests began to plateau around nestling day 12, there was little difference in weights (Fig. 4). The nestling period of two-chick (16.3 days) and one-chick (16.6 days) nests did not differ (one-way ANOVA;  $F_{1,55} = 0.36$ ,  $P = 0.55$ ).

After fledging, males were responsible for 81% of the feedings, females accounted for 8%, and an unidentified parent or helper accounted for 11% ( $n = 62$  feedings at 10 nests). Fledglings remained dependent on parents for 3–5 weeks after fledging ( $n = 73$  nests). During this period no young were observed >100 m from the nest site.

**Reproductive effort and success.**—Nesting effort and productivity differed among years (Table 2). In 1996 ( $n = 12$  territories) and 1997 ( $n = 14$  territories), median nesting effort was three nests per territory. In 1998, a relatively poor year, the nesting season was restricted to 4 months ( $n = 22$  territories) with a single nesting attempt being the median effort among closely monitored territories. The

interval between nesting attempts was  $10.2 \pm 4.0$  days (range = 5–18 days,  $n = 12$  nest-renest periods with exact dates known) following nesting success or failure. The outcome of the first nest did not affect the time interval between nest attempts ( $t_{10} = -0.12$ ;  $P = 0.91$ ). The most prolific pair fledged seven young from four (of five total) nesting attempts.

Daily probability of survival (3 year mean  $\pm$  SE) during the incubation period was  $0.949 \pm 0.032$  ( $n = 633$  egg-days [43 nests]) and during the nestling period was  $0.980 \pm 0.012$  ( $n = 715.5$  nestling-days [41 nests]). The probability of a fully incubated egg hatching was  $0.864 \pm 0.052$  ( $n = 90$  eggs [45 nests]). Egg and nestling survival both showed similar dramatic decreases in the 1998 field season, while the probability that an egg incubated to term would hatch remained near the overall average (Fig. 5). The probability of survival for the egg-to-fledging period was  $0.406 \pm 0.176$  (3-year mean  $\pm$  SE).

Of 21 nest failures, we attributed 48% to predation (19% rats [probably black rats, *Rattus rattus*], 10% owls [we suspect the Short-

TABLE 2. Distribution of number of young Puaiohi fledged per territory, by breeding season (all nesting attempts known), and summary of fecundity statistics, upper Mohihi study area, Kauai, 1996–1998.

Number of young fledged	1996	1997	1998	Mean $\pm$ SD (1996–1998)
0	1	0	14	—
1	0	0	7	—
2	2	1	1	—
3	7	0	0	—
4	2	5	0	—
5	0	2	0	—
6	0	5	0	—
7	0	1	0	—
Total territories	12	14	22	16 $\pm$ 5.3
Mean fledglings/territory	2.8	4.9	0.4	2.3 $\pm$ 2.2
Young fledged/successful nest (no. nests)	1.7 (20)	1.9 (37)	1.0 (9)	1.6 $\pm$ 0.4
Nesting attempts/territory (no. attempts)	2.2 (26)	3.3 (44)	1.1 (24)	2.4 $\pm$ 1.4
Fledglings/attempt	1.4	1.7	0.4	1.1 $\pm$ 0.7

eared Owl, *Asio flammeus*, based on our observation of this species near these nests], and 19% unknown), 14% to abandonment, 5% to weather, 5% to disturbance by non-nesting Puaiohi, 5% to hatch failure, and 24% to unknown causes. Puaiohi reused historically successful nest sites. We never observed reuse of a nest site that failed to produce young ( $n =$

4 failed nests at territories in which no subsequent nesting attempt was made). We documented reuse (1–3 times) of 18 historically successful nests in 11 different territories.

*Dispersal, fidelity, and philopatry.*—Five of the 31 nestlings (16%) that we banded in 1997 exhibited territorial behavior within our study area the following year, establishing an area

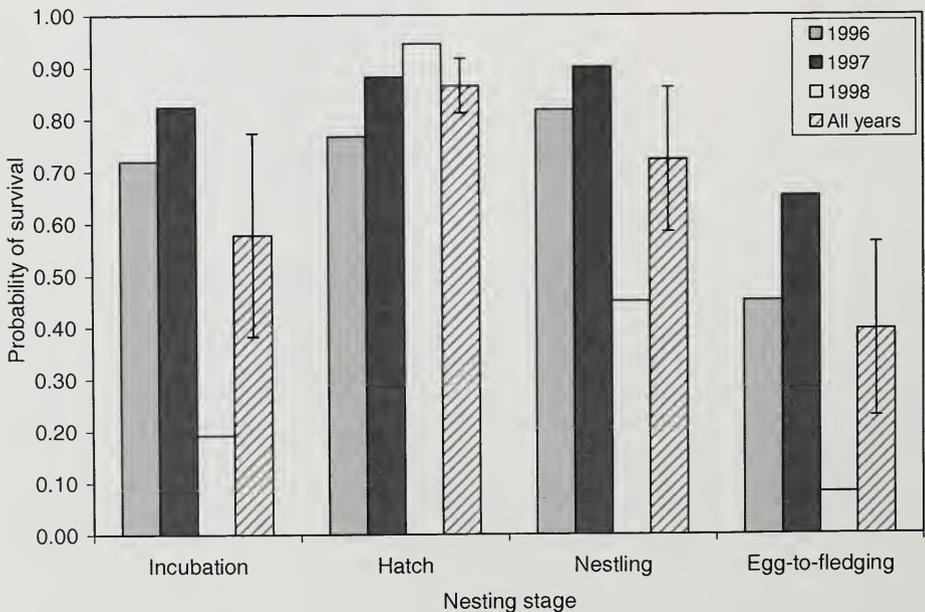


FIG. 5. Egg and nestling survival of Puaiohi for incubation, hatch, nestling, and egg-to-fledging stages by year and all years combined for nests without rat protection ( $n = 633$  egg-days [43 nests],  $n = 90$  eggs [45 nests],  $n = 715.5$  nestling-days [41 nests]). Nesting stage survival values were calculated using Mayfield daily survival rates for the incubation (13.5 days) and nestling stages (18.3 days); hatching survival is simply percent eggs hatched. Egg-to-fledging survival is the product of egg, hatch, and nestling survivals. Error bars are  $\pm$  SE.

of activity that was occupied for at least 8 weeks. Distance to natal nest from the activity center was  $279 \pm 157$  m (range = 137–538 m,  $n = 5$ ). One male succeeded in nesting 300 m from its natal site. Two others were observed within 50 m of their natal sites on at least one occasion, and two additional SY birds were documented as floaters >300 m from their natal sites.

*Survival.*—At least 25% of HY birds survived until April of the year following their banding (7 of 34 unknown sex and 2 of 2 males), and 73% of AHY Puaiohi survived until the following April (2 of 5 unknown sex, 2 of 2 females, and 4 of 4 males).

*Predators and predator control efforts.*—We protected 27 nests during 576 nest-days with rat bait stations. We monitored an additional 54 untreated nests over 1,038 nest-days. Nest fate and nest protection with rat poison were not independent ( $\chi^2 = 11.62$ ,  $df = 4$ ,  $P = 0.020$ ). At protected nests, rat predation was 0%, owl or unknown predation was 3.7%, non-predation failure was 0%, unknown failure was 0%, and 96.3% fledged  $\geq 1$  young. At unprotected nests, rat predation was 7.4%, owl or unknown predation was 13.0%, non-predation failure was 16.7%, unknown failure was 1.9%, and 61.1% fledged  $\geq 1$  young. Nest failures confirmed to have been caused by rat predation increased from 0% in 1996 and 1997 to 36% ( $n = 11$  failures) in 1998, when eggs, nestlings, and an incubating female Puaiohi were depredated by rats. However, 8% of nests in 1996 and 3% of nests in 1997 failed due to unknown causes, at least a portion of which may have been caused by rat predation. There was no evidence of rat predation at any of the nests with rat bait stations.

## DISCUSSION

The Puaiohi is a species on the brink of extinction, but it is not too late for constructive, affordable management action. It is not so rare that researchers ponder whether or not it is extinct or debate the pros and cons of removing the population from the wild. However, the situation is dire enough to cause alarm and draw the attention of managers and researchers. The Puaiohi population numbers in the hundreds, not in the thousands, and even over the few square kilometers where we found its population to be the most dense, the

Puaiohi was uncommon or rare. Predation by rats is the one clear threat that our research documented, but others loom in the background. Habitat modification through the establishment of invasive plant species and increasing exposure to avian disease both rank as serious future threats.

Through our limited surveys in three study areas, we found the Puaiohi was rare or absent over large areas of apparently suitable habitat. Expansion of the Puaiohi's current range to include all available habitat and efforts to increase the Puaiohi's density in sparsely occupied areas should rank high among efforts to manage this species' recovery. Long-term efforts to slow the establishment of invasive weeds in the Alakai and to develop techniques to eradicate or reduce rat populations there are both important to the survival of the Puaiohi. Cultivating the political will to put these steps into action is just as crucial, and without this support no rat control will ever occur in the wild, where it is needed. If all of these efforts can be implemented, they will undoubtedly have ancillary benefits in promoting the survival of other endemic species.

While researchers have focused much attention on the role of humans in the extinction or near extinction of much of Hawaii's avifauna, Kauai offers a striking example of the effect of natural events on vulnerable avian populations. Hurricanes Dot (1959), Iwa (1982), and Iniki (1992) each caused serious damage on Kauai and likely negatively affected avian populations. Notably, following Hurricane Iwa, observers documented only a few sightings of four of Kauai's five rarest species: Kamao (*Myadestes myadestinus*), Kauai Oo (*Moho braccatus*), Ou (*Psittirostra psittacea*), Nukupuu (*Hemignathus lucidus*), and Puaiohi. None except Puaiohi has been seen since Iniki.

The Puaiohi was apparently rarer than the Kamao or Ou from its discovery through the 1970s, but today it survives in numbers that appear to rival those of the past; the other species may be extinct (Perkins 1903, Richardson and Bowles 1964, Banko 1980, Sincock et al. 1984, Scott et al. 1986, Conant et al. 1998, Snetsinger et al. 1999, Reynolds and Snetsinger 2001). While life history information on Kauai's other endangered endemics is very limited (Snetsinger et al. 1998, Wakelee and

Fancy 1999, Sykes et al. 2000, Pratt et al. 2001), our data indicate that Puaiohi can be prolific breeders in comparison with Omao (Wakelee and Fancy 1999) and other Hawaiian endemics. Their high fecundity may have been one key difference between the Puaiohi and Kauai's other endangered forest birds and may help to explain their survival.

*Population structure and distribution.*—Our surveys of the upper Mohihi study area indicated that there was a steady-state breeding population for the entire period of August 1995–August 1998. In 1998, a poor breeding year overall, we noted the establishment of one new territory. In all years we noted the presence of non-breeding floaters, which acted as helpers or made unsuccessful attempts to establish territories. This indicated that the population within the study area was saturated by the end of the 1995 breeding season. Kauai was hit by Hurricane Iniki in September 1992, and USFWS/DLNR surveys in early 1993 showed no indication of Puaiohi breeding and documented only a single individual. This suggests that, at best, 1993 was a poor breeding year. Therefore, Puaiohi either survived in good numbers through Hurricane Iniki, or within two breeding seasons (1994 and 1995) the species recovered enough to saturate the upper Mohihi study area with a full complement of breeding pairs and a detectable floater population.

While our data set was small, our resightings of color-banded birds suggest young Puaiohi exhibit relatively strong philopatry and protracted juvenile dispersal. It is likely that these factors contribute to the establishment of a buffer population of non-breeders and helpers. As first documented by Ashman et al. (1984), we observed no obvious aggression by parents toward older fledglings. In fact, some fledglings assisted in raising subsequent clutches within the same year and were observed near natal territories between years. Adults also showed strong nest-site fidelity within and between years. Strong philopatry and adult nest-site fidelity combined with protracted juvenile dispersal support the theory that Puaiohi dispersal is a slow process.

Among Hawaiian forest bird species, the existence of floater populations is suspected in Omao (Wakelee and Fancy 1999) and documented in Elepaio (*Chasiempis sandwichen-*

*sis*; Vanderwerf 1998). Vanderwerf (1998) found larger and older floater populations in high-quality habitat than in marginal habitat or in populations with high mortality rates. The Puaiohi populations in the upper and lower Mohihi appear to offer the same contrast, with a well-developed floater population in the upper Mohihi and no detectable floater population in the lower Mohihi study area. While the upper Mohihi's floater population may serve as a buffer to the breeding population, the sedentary nature of these birds also prolongs the process of recovery and recolonization in areas that hold few or no Puaiohi, such as the lower Mohihi. Expansion into these areas is likely to be incremental, as only breeding birds on the periphery of a high-density area would be major contributors to range expansion, when young from their nests disperse into unsaturated habitat.

Translocation of captive-reared birds may be the most effective technique for rapidly expanding the range of this species since captive-reared birds should not demonstrate strong site fidelity—a trait that has proved to be a challenge in some translocation efforts (Fancy et al. 1997). Preliminary translocation efforts have met with mixed success (Kuehler et al. 2000, 2001; Tweed et al. 2003).

*Limiting factors affecting breeding.*—The Puaiohi's specific nest-site requirements are probably the most important limiting factor within the upper Mohihi study area. This is also probably the case at the lower Mohihi area, but the extremely low Puaiohi density there suggests that other limiting factors may also play an important role.

Most nests were constructed in cavities or on shelves in streamside cliff faces, as described by earlier researchers (Kepler and Kepler 1983, Ashman et al. 1984). Kepler and Kepler (1983) suggested that Puaiohi nest-site selection could make them less susceptible to weather effects. Our results support this conclusion as we noted only one nesting failure that we attributed to weather, despite a number of severe storms during breeding seasons.

Parents provided nestlings with equal proportions of invertebrate prey and mature fruit, suggesting a dependence on both. Lower rainfall in the winter (rainy) season of 1997–1998 may have resulted in low food availability during the 1998 breeding season. Our anec-

dotal observations suggest a scarcity of mature fruit on the Puaiohi's dominant food plants (particularly olapa; kanawao; and ohia ha, *Syzygium sandwicense*) during that period. Low food availability may have contributed to poorer condition of adults and a lack of food for nestlings in that year, either of which could have contributed to poor nesting effort.

An apparent increase in rat predation contributed to low reproductive success in 1998. While there are many possible explanations for the increase in rat predation, one reasonable theory is that a general scarcity of fruit forced the rats to search more widely for food than usual, exploring cliff walls and opportunistically finding and depredating Puaiohi nests. The combination of increased predation and a poor nesting effort reduced the number of fledglings/territory by more than 80% from that observed during each of the preceding 2 years.

*Predator control.*—Results of rat control efforts indicated that rats have a significant impact on Puaiohi nests and fledglings. Limited poisoning around active nests resulted in a higher proportion of nests that fledged young. Our discovery in 1998 of the depredation of an incubating female and her two eggs by rats emphasized that rats can impact not only nesting productivity but also the adult breeding population.

Predator control was labor intensive, as performed for this study, and would be cost prohibitive on a large scale. Given the protracted breeding season and difficult working environment, it would be exorbitantly expensive even on smaller area, such as the lower Mo-hihi study area. Large-scale rat control efforts such as those involving aerial distribution of rodenticide have the potential for substantial positive impacts (Veitch and Bell 1990, Armstrong and McLean 1995, Empson and Miskelly 1999), and these techniques are the only viable alternatives for rat control over large areas of Puaiohi habitat. However, in addition to cost and other management considerations (e.g., effects on non-target species, secondary poisoning, and potential water supply contamination), political, cultural, and social factors will need careful consideration before such methods can be attempted, even at experimental levels.

*Conclusion.*—The Puaiohi has proven itself

a survivor. Its fecundity and adaptability to captive propagation make management techniques, such as the reintroduction of captive-bred birds, potentially powerful tools in expanding the current range of the Puaiohi and increasing population density in areas where their numbers are low. However, research into limiting factors in areas of low population density will be a crucial component in the development of a successful management strategy. Effective and politically acceptable, broad-scale rat control techniques will likely play an important role in future management efforts.

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## EFFICACY OF USING RADIO TRANSMITTERS TO MONITOR LEAST TERN CHICKS

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**ABSTRACT.**—Little is known about Least Tern (*Sterna antillarum*) chicks from the time they leave the nest until fledging because they are highly mobile and cryptically colored. We evaluated the efficacy of using radio-telemetry to monitor Interior Least Tern (*S. a. athalassos*) chicks at Salt Plains National Wildlife Refuge, Oklahoma. In 1999, we attached radio transmitters to 26 Least Tern chicks and tracked them for 2–17 days. No adults abandoned their chicks after transmitters were attached. Transmitters did not appear to alter growth rates of transmitterd chicks ( $P = 0.36$ ) or prevent feather growth, although dermal irritation was observed on one chick. However, without frequent reattachment, transmitters generally did not remain on chicks <1 week old for more than 2 days because of feather growth and transmitter removal, presumably by adult terns. Although the presence of transmitters did not adversely affect Least Tern chicks, future assessments should investigate nonintrusive methods to improve retention of transmitters on young chicks and reduce the number of times that chicks need to be handled. Received 27 May 2004, accepted 30 December 2004.

Survival estimates for endangered Least Tern (*Sterna antillarum*) chicks—from hatching until fledging—are obtained primarily through indirect measures, such as ratios of observed number of fledged birds to number of successful nests (Kirsch 1996, Woodrey and Szell 1998) or estimated number of breeding pairs (Schwalbach et al. 1993). Direct measurements of survival and determining the factors that impact survival have been hindered because Least Tern chicks are semi-precocial, highly mobile, and cryptically colored. Furthermore, Least Terns nest colonially in open habitats, making undetected approach difficult. Approaches within 250 m result in alarm calls from adults, and, at that distance, chicks are difficult to see. Dugger et al. (2000) successfully used a mark-recapture technique to estimate survival of Interior Least Tern chicks (*S. a. athalassos*) nesting on islands. Because Least Tern chicks may move freely, mark-recapture techniques would be less useful in expansive nesting habitats (e.g., salt flats) than in restricted habitats (e.g., islands). In either case, neither method can reveal fac-

tors that affect survival of individual chicks. Accurate estimates of chick survivorship and cause-specific mortality are essential for determining management strategies to improve productivity of this endangered species (U.S. Fish and Wildlife Service 1990).

With varying success, adult Least Terns have been marked with patagial tags and radio transmitters. Brubeck et al. (1981) detected high rates of nest desertion after attaching patagial tags, but it was unclear whether the desertions were due to extended handling times or the tags. In two studies, adhesives were used to attach transmitters onto the backs of adult Least Terns (Massey et al. 1988, Hill and Talent 1990). In the 2-year study by Massey et al. (1988), terns marked in year one ( $n = 4$ ) were slow to return to their nests (>4 hr before return), and all terns marked in year two ( $n = 3$ ) exhibited various degrees of abnormal incubation and abandonment. In contrast, Hill and Talent (1990) found faster return rates ( $\leq 70$  min) and several transmitterd individuals resumed incubation immediately (some terns were trapped but not transmitterd). Nest desertion and nest and egg survival for radio-transmitterd terns ( $n = 20$  terns,  $n = 15$  nests) did not differ from the control group (Hill and Talent 1990).

Advances in radio-telemetry equipment have facilitated monitoring of small birds (Sykes et al. 1990, Yalden 1991). Previously, radio transmitters could be used only on mid- to large-sized animals because transmitter weights were excessive. Currently, one can

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obtain transmitters that weigh  $<1.0$  g and have a battery life of about 21 days. The life span of small transmitters limits their use for long-term monitoring of individuals, but Least Tern chicks fledge at about 20 days (Thompson et al. 1997); therefore, transmitter life is generally long enough to confirm survival to fledging.

We evaluated the efficacy of radio-telemetry to monitor Least Tern chicks from hatching until fledging by assessing the impact of carrying radio transmitters. We also report on the technical details of this method.

#### METHODS

*Study area.*—Our study was conducted from 1 June to 15 August 1999 at Salt Plains National Wildlife Refuge (SPNWR), Alfalfa County, Oklahoma ( $98^{\circ} 15' N$ ,  $36^{\circ} 43' W$ ). At this refuge, Least Terns nest on a salt flat of about 5,000 ha adjacent to Great Salt Plains Reservoir (Koenen et al. 1996). The nesting habitat is nearly level and has little vegetative cover, making detection distance of transmitter signals nearly optimal. We selected a study site at the south end of the Least Tern nesting habitat.

*Nest location.*—We located nests by searching defended territories. To reduce disturbance, we initially located nests from outside defended areas by observing adults returning to nests. If the number of potential pairs exceeded the number of nests, we conducted a systematic search of the surrounding area to locate additional nests. We marked nests with a numbered dowel placed about 10 m away from the nest cup. Dowels were placed in random directions to discourage a learned response by predators. Nests were examined visually from about 5 m away every 3–10 days until hatching. Nests that showed signs of disturbance (i.e., missing or broken eggs, etc.) were examined physically to determine cause of disturbance.

*Radio-marked chicks.*—Chicks (ages 1–3 days) were placed into a mesh bag, weighed with a hanging spring scale, and then banded with U.S. Fish and Wildlife Service aluminum leg bands. Radio transmitters were placed on the largest chick in each nest at about 2–3 days of age; we also fitted transmitters on three chicks found away from their nests. As a precautionary measure, we hooded captured

chicks to reduce stress (Hill and Talent 1990). Except for the type of glue used, we followed the transmitter attachment technique used by Hill and Talent (1990). Because cyanoacrylate glues have been linked with skin irritation and impaired skin functioning (i.e., blocked skin pores; Johnson et al. 1991), we used latex-based surgical glue (Skin Bond, Smith and Nephew, London, United Kingdom). We attached transmitters by first clipping down feathers of the interscapular region to expose the skin; then, surgical glue was brushed onto both the bare skin of the chick and the base of the transmitter. After the transmitter was in position, it was held in place for 1 min to seal the bond. When possible, surrounding feathers were glued over the top of the transmitter for camouflage and to reduce the likelihood of the transmitter being removed. Glue-on techniques have advantages over harnesses because attachment is easier (Sykes et al. 1990) and harnesses have been found to alter behavior and survival in some birds (Kenward 1987, Hubbard et al. 1998). Using a mild solvent, we removed transmitters from chicks by 17 days of age to avoid hampering chicks during fledging.

We attached 16 L.L. Electronics transmitters (model SMT-1-379-RS-T; Mahomet, Illinois) and 10 Holohil Systems Ltd. transmitters (model LB-2; Woodlawn, Ontario, Canada) to 26 chicks. Estimated life span of the transmitters was 2–3 weeks. L.L. Electronics transmitters averaged 0.8 g and measured  $0.9 \times 0.6 \times 0.4$  cm. Holohil transmitters averaged 0.6 g and measured  $1.1 \times 0.6 \times 0.2$  cm. Transmitter weight at the time of attachment was 5–8% of a chick's weight (greater than the 3% benchmark recommended by the North American Bird Banding Laboratory but less than the 10% maximum recommended by Gaunt et al. 1997), but by 6 days of age, transmitter weight was  $\leq 3\%$  of chick weight. All monitoring and handling protocols were approved under U.S. Fish and Wildlife Service Endangered Species Permit TE820283-1.

*Radio-tracking.*—The first three chicks fitted with transmitters were located once every 24 hr. When a transmitter was found to be loose, it was reattached. Because transmitters frequently became loose or detached, we located, captured, and physically examined the remainder of the chicks every 12 hr.

Chicks were tracked during morning and evening hours, when temperatures were  $<35^{\circ}$  C. We never tracked chicks during rainstorms. Once a week, we recaptured and weighed all chicks. When transmitters were removed, skin and feather condition were examined for damage.

We calculated a growth curve for transmittered chicks by weighing them weekly. Few chicks without transmitters could be found again at SPNWR; thus, growth rates of transmittered chicks could not be compared with those of untransmittered chicks from the same location. Because we were unable to locate published data on daily growth rates of Interior Least Tern chicks, we used growth data from California Least Tern (*S. a. browni*) chicks that also were captured and handled daily (Massey 1974) to estimate the impact of transmitters on growth of SPNWR chicks. We compared the straight-line segment between day 4 and 16 of each growth curve and intercepts using ANCOVA with chick age as the covariate (SAS Institute, Inc. 1996).

## RESULTS

We attached radio transmitters to 26 Least Tern chicks. Because of flooding and predation on the alkaline flat, loss of tern nests was common (e.g., Winton and Leslie 2003). Of 17 nests located in June 1999, 10 were lost before hatching and only three chicks were marked from 22 to 28 June. After adults re-nested, 23 additional chicks were marked from 24 July to 7 August 1999. Processing time per chick averaged  $16 \text{ min} \pm 1.0 \text{ SE}$ . No chicks were deserted or left unattended by adults after transmitters were attached. All chicks appeared to move normally after the transmitter was attached (Whittier 2001).

Our initial intent was to refind chicks once a day to evaluate their condition and transmitter attachment, but, of the three chicks marked in June, only one was found again and its transmitter had to be reattached twice before it was 5 days old (Table 1). The other two June chicks presumably lost their transmitters and could not be found again. Therefore, we changed our protocol to relocate chicks twice a day; transmitters were reattached whenever a light tug on the transmitter antenna revealed a partially detached transmitter. Four of 26 chicks were not found again

or died after 1 day and 4 (15%) retained their transmitters without reattachment for 3 ( $n = 2$ ), 7, and 8 days (Table 1). Transmitters requiring reattachment were prevalent in the young age classes; 18 of 26 chicks (69%)  $\leq 4$  days of age were found with partially detached transmitters (Table 1). Transmitters on these 18 chicks had to be reattached, but the number of necessary reattachments decreased as the number of monitoring days increased (Fig. 1).

Growth of chicks at SPNWR was sigmoidal ( $r^2 = 0.95$ ; Fig. 2) and averaged 2.2 g/day. Based on growth curves, predicted fledging weight of chicks at SPNWR was 40 g (assuming fledging at 20 days; Thompson et al. 1997); chicks in California weighed 40.5 g at fledging (Massey 1974). A comparison of growth rates of transmittered chicks ( $n = 20$ ) at SPNWR with untransmittered chicks ( $n = 152$ ) in California (Massey 1974) demonstrated that chick weight at 4 days of age (our study:  $11.25 \text{ g} \pm 1.76 \text{ SE}$ ; California:  $13.81 \text{ g} \pm 0.28 \text{ SE}$ ; ANCOVA,  $F_{1,24} = 4.64$ ,  $P = 0.043$ ) differed, but mean growth rate did not differ (our study: 2.3 g/day; California: 2.4 g/day;  $F_{1,24} = 0.17$ ,  $P = 0.69$ ; Fig. 2). Massey (1974) noted that weight gain and absolute weight of California tern chicks stabilized at about day 15 and varied between 35 and 40 g; chicks of the same age at SPNWR weighed between 36 and 39 g.

We examined physical condition and feather growth when we removed transmitters from chicks that died ( $n = 6$ ) or were near fledging ( $n = 7$ ). Those individuals carried a transmitter for a mean of 9 days. Two chicks fledged before we removed the transmitters and the remainder disappeared (Table 1). Only one chick exhibited any sign of skin irritation; the skin was light pink, indicating only mild irritation, and that chick successfully fledged. Two of the dead chicks did not exhibit any obvious signs indicating cause of death. The other four deaths were attributed to predation, flooding, or unusual exposure (one individual was unable to escape from a deep hoofprint). Feather growth was not impaired on any of the chicks, and feathers were not visibly damaged. Feather growth under the transmitter shifted the transmitter to a lower position on the back.

TABLE 1. Patterns of radio-transmitter retention for 26 Least Tern chicks in northcentral Oklahoma, June–August 1999. We often found chicks with partially detached transmitters that had to be reattached, but the frequency of occurrence decreased with chick age.

Chick no.	Age of chick (days)		No. of days monitored	No. of reattachments by age group in days				Total no. of reattachments	Chick fate
	Transmitter attachment	Transmitter removal		2–4	5–8	9–12	13–17		
June captures: monitored once/day									
1	2	NA <sup>a</sup>	1					0	Unknown
2	2	NA	4	2	0			2	Unknown
3	1	NA	1					0	Unknown
July–August captures: monitored twice/day									
4	2	NA	8	2	0	0		2	Unknown
5	1	NA	12	2	0	0		2	Unknown
6	2	5	3	0				0	Dead
7	2	NA	3	3				3	Unknown
8	2	NA	3	2				2	Unknown
9	4	NA	15	1	1	2	1	5	Fledged
10	2	10	8	2	1	0		3	Dead
11	1	2	1					0	Dead
12	1	NA	4	3				3	Unknown
13	2	17	15	2	1	2	0	5	Fledged
14	1	17	16	3	1	2	0	6	Unknown
15	2	5	3	1				1	Dead
16	2	13	11	2	1	0		3	Dead
17	3	16	13	1	1	1	0	3	Unknown
18	2	NA	3	2				2	Unknown
19	2	NA	1					0	Unknown
20	2	NA	8	2	1	0		3	Unknown
21	Unk <sup>b</sup>	NA	8					0	Fledged
22	Unk	Unk	3					0	Dead
23	2	NA	9	1	1	1		3	Unknown
24	Unk	NA	7					0	Unknown
25	2	15	13	3	0	1	0	4	Unknown
26	2	14	12	1	1	1	0	3	Unknown

<sup>a</sup> Not applicable: not all transmitters were removed from chicks; several individuals disappeared and two flew away with the transmitter still attached.

<sup>b</sup> Chick age was unknown when transmitter was attached.

## DISCUSSION

Radio telemetry is a reliable technique for ascertaining life-history traits of precocial and semi-precocial chicks. Various transmitter-attachment methods have been investigated for birds, including subcutaneous implants, suture and prongs, sutures, harnessed backpacks, and adhesives (Samuel and Fuller 1994, Korschgen et al. 1996, Hubbard et al. 1998, Davis et al. 1999, Burkepille et al. 2002). We do not recommend implants or either suture technique for endangered Least Tern chicks because those methods are invasive and some have led to infections (Burkepille et al. 2002). Based on apparent efforts of Least Tern adults or chicks in our study to physically remove transmitters, suture methods could result in in-

creased stress and physical trauma to chicks. Hubbard et al. (1998) recommended not using harnessed backpacks on chicks because reduced blood circulation to the wings can lead to impaired wing development that potentially could prevent flight. Adhesive methods have the advantage of (1) short handling time, (2) imposing minimal physical impairment to an individual's movement, (3) requiring no medical procedures, (4) being noninvasive, (5) minimizing the chance of infection, and (6) not causing growth impairment.

Ideally, the impact of carrying transmitters should be assessed using a reference group within the same study area (White and Garrott 1990). However, chicks at SPNWR are difficult to refind on the expansive salt flats. Dur-

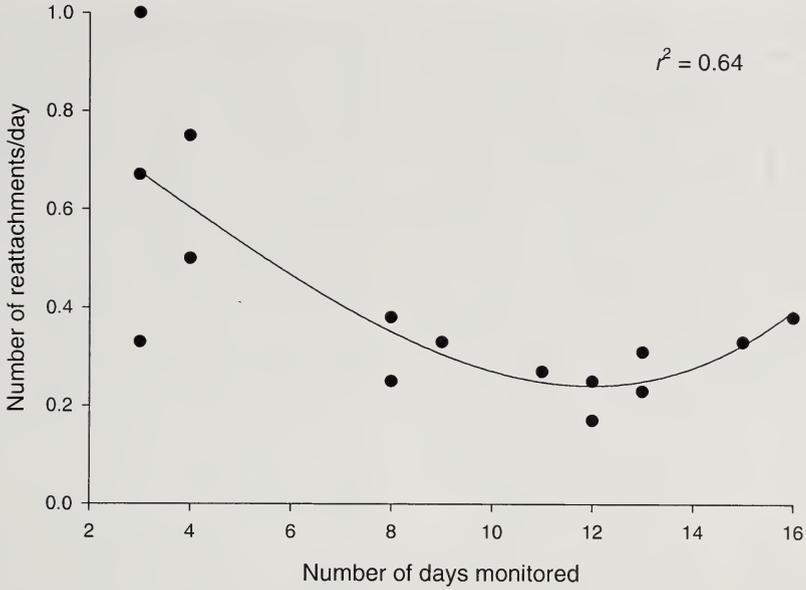


FIG. 1. Relationship between the number of days monitored and the number of reattachments necessary per day for 18 of 26 Least Tern chicks in northcentral Oklahoma, June–August 1999 (transmitters on the remaining 8 chicks were not reattached; 4 of these chicks disappeared after 1 day of monitoring).

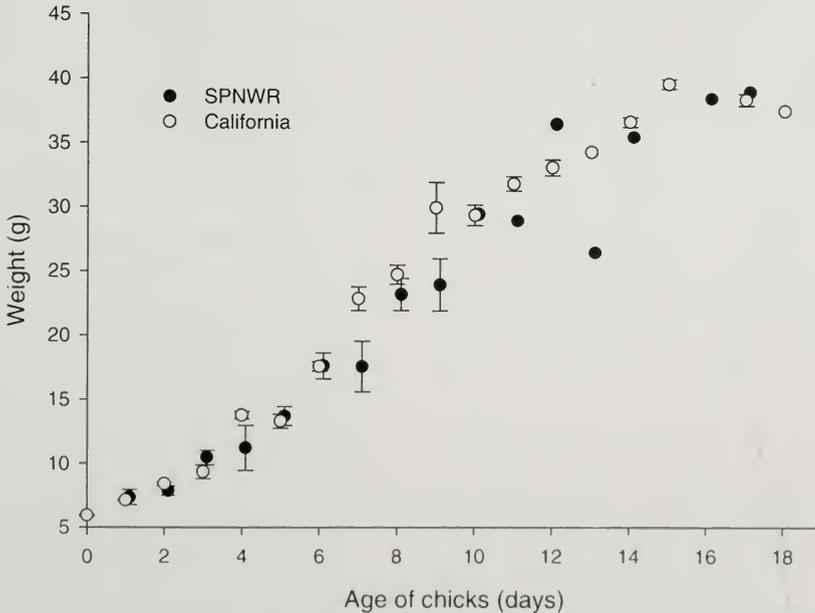


FIG. 2. Growth curves (mean weight  $\pm$  SE) of radio-transmitted Interior Least Tern chicks at Salt Plains National Wildlife Refuge, Oklahoma, and non-transmitted California Least Tern chicks (Massey 1974). At both sites, chicks were captured and handled at least once a day.

ing our study, we were unable to locate banded, untransmitted chicks or siblings of transmitted individuals. Because no detailed data were found in published literature for growth rates of Interior Least Terns, we used growth data for chicks without transmitters in California (Massey 1974). Although comparing weights of geographically disjunct populations is not ideal, we found that growth rates did not differ statistically between study groups. Frequent disturbance (up to two times per day to examine chicks and transmitters) did not prompt adult Least Terns to abandon their offspring or leave them unattended after we departed the immediate vicinity. The Kaplan-Meier estimate of survival for the transmitted chicks was 26% (Whittier 2001), which falls within the range of survival-to-fledging estimates (19–69%) for Least Tern chicks in northwestern Oklahoma (Schweitzer and Leslie 2000).

The majority of avian telemetry studies are conducted on adult or fledged birds, probably because of limitations related to transmitter weight. For this reason, little is known about the impact of the adhesive attachment technique on feather growth. Although several studies of precocial chicks have entailed using adhesives as an attachment method, or using adhesives in conjunction with another method, no mention was made of feather growth (Yalden 1991, Burkepile et al. 2002). Our results indicate that surgical glue did not disrupt feather growth in Least Tern chicks; after the glue was removed using a mild solvent, feathers were not visibly damaged. Dermal irritation was observed on only one chick, and that individual had worn its transmitter for 17 days. The low level of dermal irritation observed in this study was consistent with the findings of Sykes et al. (1990), who examined use of adhesives to attach transmitters to small passerines.

Transmitter loss was greatest when chicks were  $\leq 4$  days of age, but it also occurred in older age classes—albeit with decreasing frequency. Feather growth caused transmitters to lift from the skin and shift posteriorly down the chicks' backs. Despite transmitters shifting away from the center of gravity, transmitted chicks were able to run normally. The tendency for feather growth to move the transmitter likely contributed to the poor retention

of transmitters. Increased retention of transmitters appeared to coincide with the development of pinfeathers. Transmitters were loosened anteriorly, evidently because either parents or chicks tugged on the antennae.

Survivorship and the factors that impact survival are difficult to determine for precocial and semi-precocial chicks because they are difficult to refine. Advancements in transmitter technology have enabled production of smaller transmitters with weights that are reasonable for Least Tern chicks to carry. Those advancements provide the opportunity to more accurately assess chick survivorship and examine variables that impact survivorship for small semi-precocial chicks. Latex surgical adhesive appears to be a safe method of transmitter attachment for Least Tern chicks because it did not irritate the skin, impair feather growth, or damage feathers; however, future research should investigate methods to improve retention of transmitters. Chick growth and movement were not impaired by the presence of a transmitter.

#### ACKNOWLEDGMENTS

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## USING CANOPY AND UNDERSTORY MIST NETS AND POINT COUNTS TO STUDY BIRD ASSEMBLAGES IN CHACO FORESTS

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**ABSTRACT.**—We sampled birds with mist nets and point counts in old-growth and second-growth Chaco forest in Argentina to compare the contribution of each method to estimates of species abundance and diversity. We captured 53 species with mist nets (13 exclusively), and detected 75 species on point counts (43 exclusively). Species richness estimated by rarefaction curves did not differ between methods, except in old-growth understory, where point counts detected fewer species than mist nets. Both methods showed similar patterns of bird diversity and distribution, although point counts revealed more differences between forest layers and forest types. Mist netting contributed to the detection of cryptic or secretive species, especially in the understory, but large-bodied (>200 g) species were detected by point counts alone. Multivariate analysis discerned guilds and species associated with different forest layers and types. Point counts seem to better reflect relative abundance, whereas mist nets may be more sensitive to bird activity (e.g., movements between resources). The simultaneous use of both techniques enhances the description of bird communities, and birds' use of habitats. *Received 19 June 2003, accepted 7 November 2004.*

Mist nets and point counts have been widely used in the study of Neotropical birds (Whitman et al. 1997, Rappole et al. 1998), and a combination of the two techniques might be the most effective methodological approach for monitoring bird assemblages (Wallace et al. 1996, Gram and Faaborg 1997, Rappole et al. 1998, Poulin et al. 2000, Blake and Loiselle 2001, Wang and Finch 2002). Although point counts have been used extensively (Blake 1992, Thompson et al. 1999, Verner and Purcell 1999, Codesido and Bilenca 2000, Mills et al. 2000), they depend on the researcher's training in identification of species (Whitman et al. 1997, Blake and Loiselle 2001). Mist nets are relatively easy to use and they simplify species identification (Herrera 1978, Ralph et al. 1996); however, mist-net capture data represent species activity rather than abundance (Remsen and Good 1996), and use of mist nets is typically confined to the understory (Karr 1976, 1977, 1981; Schewske and Brokaw 1981; Blake and Rougès 1997; Gram and Faaborg 1997; Restrepo and Gómez 1998; Gardali et al. 2000), thus excluding most canopy birds (Karr 1976, Caziani 1996, Remsen and Good 1996, Rappole et al. 1998, Blake and Loiselle 2001, Wang and Finch 2002). Few investigators

have used mist nets systematically in more than one forest layer (Lovejoy 1974, Karr 1976), and none have analyzed the contribution of simultaneous mist netting and point counts in the study of bird assemblages in different forest layers.

In this study, we compare the results obtained from mist nets and point counts as part of a larger study to compare the vertical distribution of birds and their resources between two different forest habitats in the semi-arid Chaco. The vertical distribution of birds has mainly been studied using different techniques in multi-layered tropical rainforests with high tree canopies (Anderson and Shugart 1974, Lovejoy 1974, Karr 1976, Loiselle 1987, Terborgh et al. 1990, Blake and Loiselle 2001, Winkler and Preleuthner 2001). The subtropical, semi-arid Chaco forest, with its low tree canopy and relatively simple vertical structure, provides an ideal system for testing the use of canopy and understory mist nets and point counts to study bird assemblages. Our objectives in this study were to (1) evaluate the use of canopy mist nets in a semi-arid forest with a low tree canopy, (2) compare estimates of species richness and abundance based on point counts and mist nets, and (3) compare the ability of point counts and mist nets to detect differences in bird assemblages between canopy and understory, and between two forest types (old-growth forest and second-growth forest).

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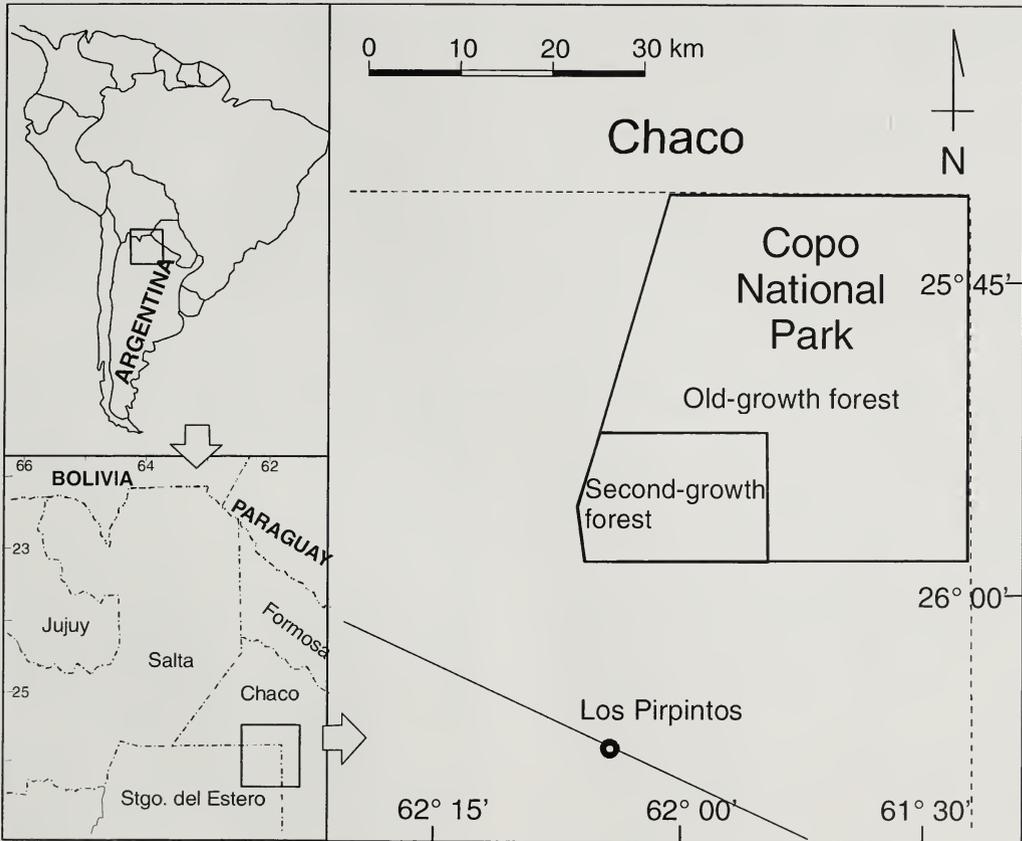


FIG. 1. Copo National Park study area, Santiago del Estero province, northwestern Argentina.

## METHODS

**Study area.**—Copo National Park (114,000 ha, 160 m elevation) is located in Santiago del Estero Province, Argentina ( $25^{\circ} 55' S$ ,  $62^{\circ} 05' W$ ). The area is considered a key preserve for threatened Neotropical birds (Wege and Long 1995). Extensive stands of old-growth forest persist in the northern and eastern portions of the park; the southwestern sector was selectively logged in the 1950s (Fig. 1). The climate is seasonal, with 80% of annual rainfall occurring October–March. Summer temperatures in the region are extreme (mean maximum =  $47^{\circ} C$ ; Prohaska 1959).

The dominant vegetation is thorny, semi-deciduous forest dominated by quebracho colorado santiagueño (*Schinopsis lorentzii*), quebracho blanco (*Aspidosperma quebracho-blanco*), and mistol (*Zizyphus mistol*), and is interrupted by belts of natural grasslands associated with ancient river beds. The under-

story is a dense, shrubby layer (4 m mean height), dominated by sacha poroto (*Capparis retusa*; Protomastro 1988, Tálamo and Caziani 2003). Above this layer, mistol forms a sparse layer with both quebracho species, the tops of which attain a mean height of 12 m (López de Casenave et al. 1998).

**Sampling.**—We conducted bird surveys during six periods in Copo National Park (December 1998, March 1999, August 1999, December 1999, April 2000, and September 2000) in two forest types: old-growth and second-growth (i.e., 50 years after selective logging). In each forest type, we established eight mist-net stations, 100 to 200 m apart, four in the understory (0–3 m above ground) and four in the canopy (5–8 m above the shrubby layer). At each station, we placed one mist net, 12.5 m long  $\times$  2.8 m high (36-mm mesh). We operated nets for 3 days in each type of forest during each survey period (Ralph et al.

1996), except for the second-growth forest in December 1998, when only 1 day of sampling occurred; thus, we mist-netted for 18 days in old-growth and 16 days in second-growth. We opened nets before sunrise and operated them for 3–6 hr/day when possible, but we often had to close nets early due to temperature and weather conditions. Canopy nets were installed with a modification of the technique described by Humphrey et al. (1968), with trees supporting a system of pulleys and ropes. We added vertical aluminum poles for additional support. For each bird captured, we recorded species, forest type, layer, date, time, weight, standard morphological measurements, and sex. Each bird was banded with National Park Administration aluminum bands and released. Data were expressed as captures per 100 mist-net hr (MNH), including recaptures (Bibby et al. 1992).

We established eight point-count stations, at least 400 m apart, in each of the two forest types. In each survey period, we twice visited all point-count stations to conduct 10-min unlimited-distance point counts on 2 consecutive days, reversing the order of visits to avoid time-of-day bias. Surveys began at sunrise and were completed within 3 hr (Bibby et al. 1992, Ralph et al. 1996, Gram and Faaborg 1997). During each point count, we recorded species and number of individuals detected by sight or sound, and the forest layer in which each individual was detected for the first time. Layers were defined as understory (0–4 m) and canopy (>4 m). Every individual seen or heard was recorded only once, so that observations per layer were considered to be independent, and layers at a single station were treated as separate treatments in the analysis. Birds over-flying the canopy were not included. Results are expressed as number of detections per 10 min (Bibby et al. 1992). One observer (EJD) conducted all point counts.

Guilds were defined according to previous studies in the area (Caziani 1996, López de Casenave et al. 1998) as follows: omnivores, carnivores, nectivores, terrestrial granivores, arboreal granivores, terrestrial insectivores, bark insectivores, foliage insectivores, short-flight insect hunters, long-flight insect hunters, frugivores, and undergrowth granivores.

*Statistical analyses.*—We compared species richness using rarefaction curves, given that

the number of individuals in a sample can influence the number of recorded species (James and Rathbun 1981). Rarefaction estimates the number of species expected from different samples, based on multiple random sampling of increasing abundance. Curves were built with 1,000 iterations for each abundance level using Program EcoSim (Gotelli and Entsminger 2002). The program calculates a 95% confidence interval for each mean species richness value.

For each survey method, we compared total records, total records by guild, and records of the most common species. We employed a factorial design with forest type as the first factor (two levels: old-growth forest and second-growth forest,  $a = 2$ ) and layer as the second factor (two levels: understory and canopy,  $b = 2$ ). Replicates by treatment (forest  $\times$  layer) were the four mist-net stations ( $r = 4$ ) and the eight point-count stations ( $r = 8$ ), respectively. Seasonality was not considered; however, the six survey periods were included in the analysis as repeated measures, using a split-plot ANOVA (Von Ende 1993). Assumptions of ANOVA were satisfied by logarithmic transformation of the data. For the between-factor comparisons, error degrees of freedom were calculated as  $[a \times b \times (r - 1)]$ ; due to the collapse of three nets in one survey period (two canopy nets and one understory net), 3 degrees of freedom were subtracted from the error degrees of freedom.

*Detrended correspondence analysis.*—To describe the association of bird species and guilds with treatments (forest  $\times$  layer), we applied Detrended Correspondence Analysis (DCA) to the matrices of total captures by net stations and total detections by point-count stations using Program PC-ORD (Gauch 1982, McCune and Mefford 1997). DCA is an ordination technique that groups species and stations in a two-dimensional scatterplot, where species lying close together show similar use of forest layers and forest types, and forest layers and types lying close together have similar avian communities.

## RESULTS

We recorded 91 species, including 13 recorded only with mist nets and 43 only with point counts. An additional 17 species were observed either flying over the study area or

TABLE 1. Mist-net hr (MNH), captures (C), captures per 100 MNH, species richness (S), and mean captures  $\pm$  SE by forest type and by layer, Copo National Park, northwestern Argentina, 1998–2000. MNH is lower in second-growth forest because we lost one canopy mist net in three sample periods because of extreme weather, and we had only 1 day of sampling in December 1998.

Layer	Old-growth forest					Second-growth forest				
	MNH	C	C per 100 MNH	S	Mean $\pm$ SE	MNH	C	C per 100 MNH	S	Mean $\pm$ SE
Understory	360	134	37.2	40	49.6 $\pm$ 7.5	229	90	39.2	35	51.8 $\pm$ 8.8
Canopy	320	178	55.6	37	41.6 $\pm$ 6.5	202	105	52.0	37	41.1 $\pm$ 7.6
Total	680	312	45.8	45	45.6 $\pm$ 6.9	431	195	45.2	46	46.4 $\pm$ 8.1

outside of the sampling periods. The two methods combined detected 80% of the species reported for forest habitat in the area (Caziani 1996).

We captured 507 birds of 48 species in 1,111 MNH (34 days; Table 1). Recaptures represented 1.53% of total captures. We detected 907 individuals of 78 species in 32 point-count hr (Table 2). Considering both mist-net captures and point-count detections, 10 species were exclusive to old-growth forest, 15 to second-growth forest, 28 to the canopy, and 29 to the understory. Raptors (Accipitridae and Falconidae), parrots and parakeets (Psittacidae), woodcreepers (Dendrocopidae), warblers (Parulidae), tanagers (Thraupidae), and caciques (Icteridae) dominated canopy records. Tinamous (Tinamidae), seriemas (Cariamidae), nightjars (Caprimulgidae), antbirds (Formicariidae), and tapaculos (Rhinocryptidae) were recorded only in the understory. Expected species richness (Fig. 2) was similar between census methods, forest layers, and forest types, as confidence intervals on rarefaction curves overlapped in all cases, with the exception of point counts in old-growth forest understory, which had significantly fewer species.

Using mist nets, the species most often detected were Creamy-bellied Thrush (*Turdus*

*amaurochalinus*), White-crested Elaenia (*Elaenia albiceps*), Small-billed Elaenia (*E. parvirostris*), Red-crested Finch (*Coryphospingus cucullatus*), and Red-eyed Vireo (*Vireo olivaceus*), representing 48% of total captures. Only White-crested Elaenias were captured more frequently in old-growth forest ( $F_{1,9} = 13.65$ ,  $P = 0.005$ ). Bark insectivores were captured more often in the understory than the canopy ( $F_{1,9} = 5.27$ ,  $P = 0.047$ ), but no other guild showed a significant difference between layers.

Using point counts, the species most often detected were Chaco Chachalaca (*Ortalis canicollis*), Masked Gnatcatcher (*Poliophtila dumicola*), Picazuro Pigeon (*Columba picazuro*), Stripe-backed Antbird (*Myrmorchilus strigilatus*), and Creamy-bellied Thrush, representing 52% of total detections. The first three species were detected more often in second-growth forest ( $F_{1,28} = 4.47$ ,  $P = 0.040$ ;  $F_{1,28} = 3.76$ ,  $P = 0.060$ ; and  $F_{1,28} = 4.61$ ,  $P < 0.001$ , respectively); Chaco Chachalaca was more abundant in the canopy ( $F_{1,28} = 10.03$ ,  $P = 0.004$ ), and Stripe-backed Antbird and Creamy-bellied Thrush were more abundant in the understory ( $F_{1,28} = 21.40$ ,  $P < 0.001$  and  $F_{1,28} = 7.7$ ,  $P = 0.009$ ). Total point-count detections per 10 min were significantly higher in old-growth forest ( $F_{1,28} = 6.85$ ,  $P =$

TABLE 2. Point count hours (PCH), total birds detected (D), detections per 10 min, species richness (S), and mean detections  $\pm$  SE, by forest type and layer, Copo National Park, northwestern Argentina, 1998–2000.

Layer	Old-growth forest					Second-growth forest				
	PCH	D	D per 10 min	S	Mean $\pm$ SE	PCH	D	D per 10 min	S	Mean $\pm$ SE
Understory	8	222	4.6	29	29.7 $\pm$ 3.3	8	175	3.6	38	24.1 $\pm$ 1.9
Canopy	8	289	6.0	40	35.6 $\pm$ 2.9	8	221	4.6	41	34.1 $\pm$ 6.7
Total	16	511	10.6	52	76.8 $\pm$ 4.4	16	396	8.2	61	73.5 $\pm$ 7.1

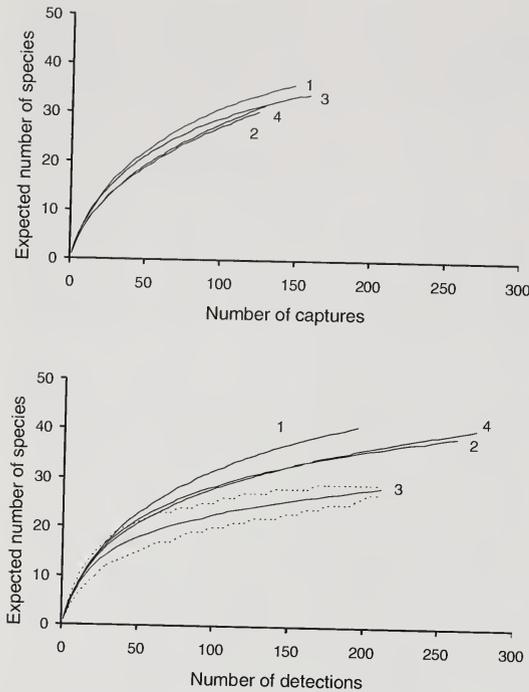


FIG. 2. Species rarefaction curves show the expected number of species related to the number of captures in mist nets (top) and number of detections in point counts (bottom), by forest type and layer, Copo National Park, northwestern Argentina, 1998–2000. Dotted lines correspond to the 95% confidence interval for the expected number of species detected in old-growth forest understory. Confidence intervals on other curves were omitted for clarity. (1) Second-growth forest understory, (2) second-growth forest canopy, (3) old-growth forest understory, and (4) old-growth forest canopy.

0.014) and in the canopy ( $F_{1,28} = 4.98$ ,  $P = 0.034$ ; Table 2). Short-flight insect hunters, omnivores, and terrestrial granivores were all more abundant in the understory than in the canopy ( $F_{1,28} = 7.40$ ,  $P = 0.011$ ;  $F_{1,28} = 42.37$ ,  $P < 0.001$ ; and,  $F_{1,28} = 32.8$ ,  $P < 0.001$ , respectively). Bark insectivores and arboreal granivores were more abundant in the canopy ( $F_{1,28} = 55.07$ ,  $P < 0.001$ ;  $F_{1,28} = 22.55$ ,  $P < 0.001$ ). Terrestrial insectivores had higher abundances in second-growth forest ( $F_{1,28} = 7.4$ ,  $P < 0.001$ ), and undergrowth granivores were more abundant in old-growth forest ( $F_{1,28} = 18.8$ ,  $P < 0.001$ ).

DCA analysis applied to the point-count matrix (Fig. 3A) clearly distinguished bird assemblages between canopy and understory (Axis 1), and between old-growth and second-

growth forest, especially for understory (Axis 2). Bark insectivores and arboreal granivores appeared to be associated with the canopy for both forest types. Terrestrial granivores characterized the understory. DCA analysis applied to mist-net captures (Fig. 3B) also distinguished bird assemblages between layers and forest types, though less clearly. Only two guilds (bark insectivores and short-flight insect hunters) showed clear patterns; both guilds were associated with the canopy.

## DISCUSSION

In agreement with other studies, we detected more species with point counts than with mist nets (Gram and Faaborg 1997; Whitman et al. 1997; Blake and Loiselle 2000, 2001; Wang and Finch 2002). The major advantage of mist nets is that less experience in species identification is required, and, in fact, censusing with mist nets may aid the observer in gaining familiarity with different species (Ralph et al. 1995). In the understory, mist nets can be more effective than point counts in detecting smaller birds, or those with more cryptic plumage or secretive behavior (Mason 1996; Rappole et al. 1998; Blake and Loiselle 2000, 2001; Wang and Finch 2002). However, canopy mist nets require greater effort to install (Humphrey et al. 1968, Meyers and Pardieck 1993), and they are more affected by weather (e.g., wind entanglement in treetops). Canopy nets do overcome one of the principal deficiencies of mist nets: only sampling the lowest forest layer (Blake 1992, Remsen and Good 1996, Rappole et al. 1998). Some species, however, are not detectable with nets due to size or behavior (Blake and Loiselle 2001, Wang and Finch 2002).

On the other hand, point counts are easier to conduct, and are more efficient in terms of data collected per unit of effort (Bibby et al. 1992). However, point-count detections may vary according to foliage density, visibility, and the transmission and perception of sounds during censuses (Schieck 1997). This may account for the lower richness estimate obtained by point counts in the understory of old-growth forest (Fig. 2), the layer with highest foliage density (Lopez de Casenave et al. 1998; EJD and SMC unpubl. data). Furthermore, point counts require training in species identification, particularly knowledge of vo-

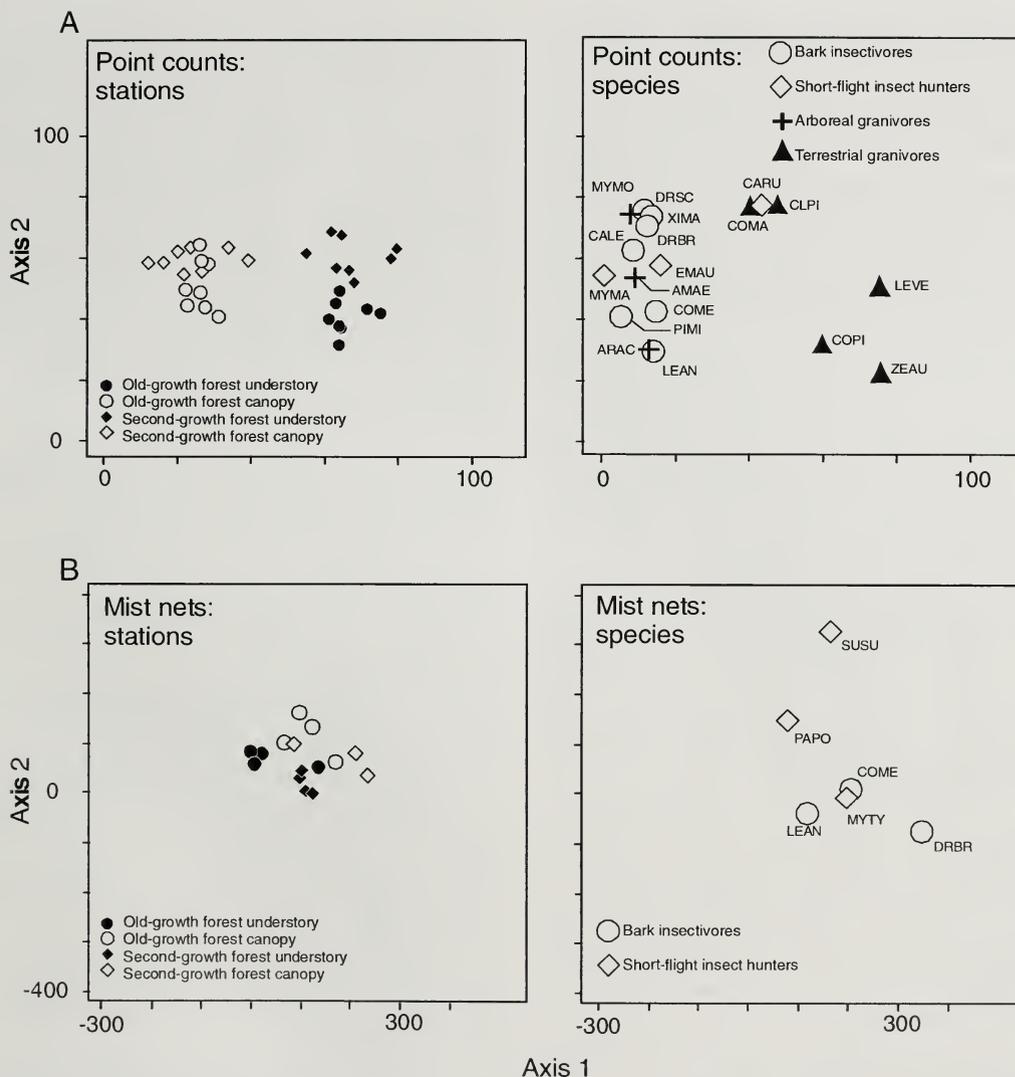


FIG. 3. Detrended Correspondence Analysis (DCA) using (A) point-count and (B) mist-net matrices, Copo National Park, northwestern Argentina, 1998–2000. For clarity, we show only species belonging to guilds that showed strong associations with forest type or layer. Axis 1 appears to be associated with layers and axis 2 with forest type. Species codes: AMAE (*Amazona aestiva*), ARAC (*Aratinga acuticaudata*), CALE (*Caupephilus leucopogon*), CARU (*Casioris rufa*), CLPI (*Columba picazuro*), COMA (*C. uaculosa*), COME (*Colaptes melanolaemus*), COPI (*Columbina picui*), DRBR (*Dryornis bridgesii*), DRSC (*Dryocopus schulzi*), EMAU (*Eupidononius aurantioatrocristatus*), LEAN (*Lepidocolaptes angustirostris*), LEVE (*Leptotila verreauxi*), MYMA (*Myiodynastes uaculatus*), MYMO (*Myiopsitta monachus*), MYTY (*Myiarchus tyrannulus*), PAPO (*Pachyrhamphus polychopterus*), PIMI (*Picooides mixtus*), SUSU (*Suiriri suiriri*), XIMA (*Xiphocolaptes major*), and ZEAU (*Zenaida auriculata*).

calizations (Bibby et al. 1992, Ralph et al. 1996); consequently, detection ability can vary significantly among observers (Rappole et al. 1998, Nichols et al. 2000). Similarly, species differ in characteristics that affect detection and identification (Nichols et al. 2000,

Wang and Finch 2002), thereby increasing the variability of results.

Mist-net captures may reflect differences in activity, whereas point counts more likely reflect variation in abundance (Remsen and Good 1996). In some cases, however, relative

abundances obtained by the two methods are similar (Wang and Finch 2002). In Chaco forest, we believe that mist-net captures reflected bird movements, whereas other activities (e.g., nesting, courtship, displays, and territorial singing) were more likely to be detected during point counts. Depending on the layer where activities occur, the probability of detection can vary greatly between methods (Blake and Loiselle 2000, 2001). For example, woodcreepers were detected more frequently in the canopy with point counts, but a larger number were captured with mist nets in the understory, where birds move from trunk to trunk. In contrast, most woodpeckers were only detected during point counts, as they tended to move between treetops above our canopy nets. These patterns are clear in the DCAs. The point-count DCA remained similar, even when we repeated the analysis with the same number of replicates as that of mist nets, selected at random. The poor explanatory power of the mist-net DCA was likely due to few or no captures of birds from some guilds (i.e., arboreal granivores, carnivores, long-flight insect-hunters).

The utility of point counts and mist nets is influenced by vegetation structure (Blake and Loiselle 2000, 2001; Wang and Finch 2002): the relative contribution of each method may vary in different environments. In tall forests, canopy birds are poorly represented by both understory mist nets and point counts (Blake and Loiselle 2001). In Chaco forests, where canopies are lower, the point-count census technique was adequate and the contribution of canopy nets was less significant. Only understory mist nets captured species not detected on point counts. Nonetheless, the usual disadvantage of underestimating canopy birds during mist-netting efforts was at least partially avoided by using canopy nets (e.g., canopy nets accounted for higher proportions of frugivores). Finally, comparisons of captures and counts among layers provided evidence of movement between resource patches.

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# Short Communications

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## Eastern Bluebird Provisions Nestlings with Flat-headed Snake

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**ABSTRACT.**—There are few published reports of Eastern Bluebirds (*Sialia sialis*) taking vertebrate prey or provisioning their young with vertebrates. We report finding a dead flat-headed snake (*Tantilla gracilis*) in an Eastern Bluebird nest. Flat-headed snakes feed primarily on soft-bodied invertebrates; thus, it is unlikely that the snake was attempting to depredate the bluebird nestlings. Moreover, flat-headed snakes are fossorial and rarely occur in open habitats. Therefore, the snake was most likely captured by one of the adult bluebirds and brought to the nestlings as a food item. Received 7 November 2003, accepted 4 November 2004.

With the exception of shrikes (Family Laniidae), most passerines generally feed insects and small fruits to their developing nestlings (Pinkowski 1978, Ehrlich et al. 1988, Gowaty and Plissner 1998). However, Eastern Bluebirds (*Sialia sialis*) occasionally have been reported to prey on vertebrates, such as shrews (*Sorex* spp.; Pinkowski 1974), snakes (unidentified species; Flanigan 1971), and skinks (*Eumeces* spp.; Pitts 1978). In a box-nesting population of Eastern Bluebirds in Oklahoma, Bay and Carter (1997) reported six different pairs of adults taking ground skinks (*Scincella lateralis*) as food items for nestlings over a period of several breeding seasons. Although provisioning bluebird nestlings with vertebrate food items has been observed, it is considered a rare phenomenon in passerines (Ross 1989).

During the 2003 breeding season, we monitored 20 nest boxes at Tyler State Park, in an upland, open shortleaf and loblolly pine (*Pinus echinata*, *P. taeda*, respectively) forest approximately 22 km north of Tyler, Smith County, Texas. The nest boxes, which were attached to metal T-posts 1.5 m from the ground, were monitored weekly and nesting activity was recorded.

On 6 May 2003, we found a small (8.3 cm in length), dead flat-headed snake (*Tantilla gracilis*) in an Eastern Bluebird nest. The snake was intact and slightly desiccated, but did not have any visible external injuries. The nest had been previously checked on 29 April and contained nestlings (12–13 days old) that were within 3 days of fledging.

During visits to nest boxes at this site, we usually did not observe provisioning of young by adult birds nor did we observe Eastern Bluebirds taking prey resembling small snakes. However, we have removed Texas ratsnakes (*Elaphe obsoleta*) that had preyed on nestling Eastern Bluebirds in our nest boxes (SCB and DWP unpubl. data), but these are the only snakes we had previously recorded in nest boxes at this site.

The flat-headed snake is a small, docile, burrowing snake that eats a variety of invertebrates, such as centipedes and soft-bodied insect larvae (Werler and Dixon 2000). Adult flat-headed snakes typically range in size from 17.8 to 20.3 cm, and usually are found beneath rocks (Ford et al. 1991, Conant and Collins 1998, Werler and Dixon 2000). According to Werler and Dixon (2000), flat-headed snakes (over 500 specimens) were never caught out in the open during a long-term study of this species in Kansas. Ford et al. (1991) examined snake diversity in northeastern Texas and found a very low abundance of flat-headed snakes. They concluded that due to the burrowing nature of this species, it may be more abundant at a particular site than trap rates might indicate. At Tyler State Park, the abundance of flat-headed snakes is unknown. Due to the natural history (i.e., fossorial habits and invertebrate prey) and small size of this particular snake, it is unlikely that it was capable of climbing the T-post and entering the nest box on its own.

The primary foraging mode of Eastern Bluebirds is to scan the ground from a perch and then drop to the ground to subdue their

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prey (Pinkowski 1977). The adult Eastern Bluebird would have had no trouble subduing a prey item of this size and may have mistaken the snake for a large insect larva. Additionally, the nestlings would have had no difficulty consuming food of this size. Therefore, it appears that one of the adult Eastern Bluebirds captured this small snake on the ground and then brought it to the nest as a food item for the nestlings. It is unclear why the snake was not eaten by the nestlings, although it may be because the snake was brought to the nest very near the time of fledging.

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## Sapsuckers Usurp a Nuthatch Nest

Christine A. Rothenbach<sup>1,2</sup> and Christopher Opio<sup>1</sup>

**ABSTRACT.**—We document for the first time a Red-naped Sapsucker (*Sphyrapicus nuchalis*) usurping the nest of a Red-breasted Nuthatch (*Sitta canadensis*). A nuthatch nest in the incubation phase was usurped by a male Red-naped Sapsucker on 23 May 2003, and a sapsucker nest was initiated in the cavity on 1 June. Red-naped Sapsuckers are primary cavity excavators that normally nest in live and dead quaking aspens (*Populus tremuloides*) infected with heart rot fungus (*Fomes* spp.). Red-breasted Nuthatches are weak ex-

cavators that most commonly nest in broken-topped conifer snags. Nest usurpation was likely due to a shortage of suitable nest sites in our study plot. *Received 26 April 2004, accepted 9 December 2004.*

The most common avian nest usurpers in North America are secondary cavity-nesting species, especially the European Starling (*Sturnus vulgaris*) and House Wren (*Troglodytes aedon*) (Short 1979, Lindell 1996, Doherty and Grubb 2002). Although nest usurpation has also been documented among cavity-excavators, both types are thought to be a consequence of a shortage of nest sites, com-

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bined with niche convergence (Short 1979, Lindell 1996).

We document for the first time a Red-naped Sapsucker (*Sphyrapicus nuchalis*) usurping the nest of a Red-breasted Nuthatch (*Sitta canadensis*). The usurpation occurred during a research project on nuthatch responses to restorative treatments in ponderosa pine (*Pinus ponderosa*) forests in the Blue Mountains of northeastern Oregon. The study area was located in the Wallowa-Whitman National Forest north of Enterprise, Oregon (45° 37' N, 117° 15' W). The stand, located on a ridge top at an elevation of 1,170 m, was dominated by ponderosa pine interspersed with Douglas-fir (*Pseudotsuga menziesii*). The area had undergone a prescribed understory burn in the fall of 2000, and the forest canopy was relatively open.

On 27 April 2003, we discovered a Red-breasted Nuthatch nest in a broken-topped ponderosa pine snag. The snag was 6.5 m tall, had 75% of its bark remaining, and its diameter at breast height was 28.6 cm. All branches were present but partially broken off, and there were no outward signs of heart rot fungus (*Fomes* spp.). On the snag we observed exit holes of bark beetles (*Dendroctonus* spp.) but not wood-boring beetles (Cerambycids or Buprestids). The cavity was 6 m above ground and lacked the layer of pitch that is occasionally found around nuthatch nest cavities. Judging by the dark color around the cavity entrance and the lack of fresh wood chips at the base of the snag, the cavity was excavated at least 1 year prior to the 2003 nesting season. The snag was located within 10 m of the edge of a large (>50 ha) patch of forest and within 20–80 m of several other snags that appeared to have undergone a similar amount of decay.

On 27 April, we watched nuthatch adults bring nesting material to the nest for 25 min. On 5 May, we believed that the nuthatches were not yet incubating because we frequently observed the female outside the cavity. During 30 min of observation on 11 May, the male brought food to the cavity entrance three times and fed the incubating female. After this visit, we checked the nest at least every 3 days.

On 23 May, near the expected hatch date, we observed a male Red-naped Sapsucker enlarging the entrance to the nest. Within 20 min, the sapsucker had enlarged the cavity en-

trance sufficiently to access the nesting material inside. The sapsucker pulled out nesting material and eggshells for the next 15 min, dropping material onto the ground at the base of the snag, or flying to the limb of a nearby ponderosa pine before dumping it. Nuthatches called from  $\leq 100$  m, but they never came to within 50 m of the nest during this period.

By 28 May, both the female and male sapsuckers were entering the nest and excavating from within the cavity. On 20 June, we confirmed the presence of sapsucker nestlings (by begging calls). The nest was still active on 28 June, but by 1 July, there was no activity. The nest failed approximately 13 days after the sapsucker eggs hatched.

Red-naped Sapsuckers most often nest in live and dead quaking aspen (*Populus tremuloides*; Martin and Eadie 1999) infected with heart rot fungus (*Fomes igniarius*; Bent 1939, Crockett and Hadow 1975), or in western larch (*Larix occidentalis*; McClelland and McClelland 2000) and birch (*Betula* spp.; Kilham 1971, Tobalske 1992). Red-breasted Nuthatches typically excavate their own cavities in broken-topped conifer snags in temperate coniferous and mixed coniferous forests (Steeger and Hitchcock 1998, Ghalambor and Martin 1999). A shortage of potential nest sites within a given area, however, can cause the convergence of species on a particular nest niche (Lindell 1996). This convergence can lead to nest competition, including nest usurpation (Lindell 1996). Emphasis should be placed upon documenting incidental occurrences of nest usurpation in order to increase our understanding of this phenomenon.

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## The Nest and Nestlings of the Wing-banded Antbird (*Myrmornis torquata*) from Southern Guyana

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**ABSTRACT.**—The Wing-banded Antbird (*Myrmornis torquata*) is a poorly known subsocial passerine found in lowland Amazonian forests. Here, we present new information about the nest and nestlings of this enigmatic species. Our findings differ from previous observations and notes on clutch size. *Received 2 July 2004, accepted 9 December 2004.*

The Wing-banded Antbird (*Myrmornis torquata*) has long mystified avian systematists as to its taxonomic affinities. Prior to discovery of the first Wing-banded Antbird nest by Tostain and Dujardin (1988), some authors (Peters 1951, Meyer de Schauensee 1966) aligned this species with the ground antbirds (Formicariidae). The nest discovered by Tostain and Dujardin (1988) was placed off the

ground in the fork of a small tree, providing additional natural history evidence that the Wing-banded Antbird should be classified as a member of the typical antbird (Thamnophtidae) assemblage. The natural history and population centers for this species, however, remain poorly known (Zimmer and Isler 2003: 671). Zimmer and Isler (2003) also suggest that the Guianan region may be a productive region for the study of Wing-banded Antbirds. Here, we present additional information on the nest of the Wing-banded Antbird with the first description of nestlings and additional behavioral notes from Guyana.

During an avifaunal and botanical survey of the Acari Mountains in extreme southern Guyana (1° 20' N, 58° 56' W, 250 m in elevation, 3 September 1998), we photographed the nest and collected the nestlings and adults of Wing-banded Antbirds. Birds and the nest were found in *terra firme* forest approximately 5 km south of the Sipu River. The nest was found on the slope of a small hill about 0.5 km from a small stream in tall humid forest (30–50 m in height) with a moderately dense understory.

Adult birds were observed foraging on the

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FIG. 1. Nest and nestlings of the Wing-banded Antbird, 3 September 1998, southern Guyana (photo by C. M. Milensky).

ground and giving soft “chip” contact calls. As we approached the birds, we noticed they were foraging around a nest. The nest was located in the fork of a sapling that was 1 m tall and 1 cm in diameter (Fig. 1). Nest measurements were outside diameter (15–17 cm), inside diameter (4–10 cm), inner cup depth (2–3 cm), and outer cup height (4–5 cm). The nest was constructed of loosely woven twigs with a lining of rootlets.

The two nestlings were featherless, but small feather sheaths were beginning to emerge (Fig. 1). Pinfeathers of most typical antbird nestlings begin to erupt 2–3 days after hatching, so we suspected that these birds had hatched recently (Zimmer and Isler 2003). Both adults were collected and made into study skins; specimens are stored at the University of Kansas in Lawrence (male: KU 90355, 50 g, testes  $6 \times 3$  mm; female: KU 89793, 45 g, ovary  $8 \times 4$  mm, largest ova 2 mm, oviduct convoluted 2 mm). The nestlings were collected and preserved in formaldehyde (KU 89671, 89672). Both adults had insects

in their stomachs. The nestlings weighed 9.6 and 9.8 g; the irides, tarsi, and maxilla were brown, the foot pads were gray, and the mandible was orange with a brown tip.

Tostain and Dujardin (1988) reported finding Wing-banded Antbird nests and families near the equator with only one egg or fledgling, respectively, and pointed out that this is unique among typical antbirds, which normally lay two eggs per clutch. They suggest that this may have been due to a positive relationship between clutch size and latitude, with reduced clutches near the equator, similar to that reported for Black-spotted Bare-eyes (*Phlegopsis nigromaculata*; Willis 1979). Our observation contradicts this idea and suggests that factors other than latitude influence clutch size in Wing-banded Antbirds. Tostain and Dujardin (1988) also reported finding nests and fledglings from July–October, and our September record is congruent with this putative breeding season.

When foraging, Wing-banded Antbirds have been observed using their bills to probe

through leaf litter, and using jumping motions to move leaves (Tostain and Dujardin 1988, Zimmer and Isler 2003). The male and female we observed appeared to be scratching through the leaf litter with their feet, throwing leaves up to 20 cm in the air, similar to that reported in Zimmer and Isler (2003). The species' foraging behavior has been described as "deliberate and inconspicuous" (Zimmer and Isler 2003), but our observation varies a bit from this account. Although the birds were deliberate in their movements, our attention was drawn to the birds because of the loud and conspicuous manner in which they scratched through the understory. Such detectability, however, may vary with local environmental conditions (i.e., the relative dryness of the leaf litter).

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# Ornithological Literature

Edited by Mary Gustafson

THE METAZOAN PARASITE FAUNA OF GREBES (AVES: PODICIPEDIFORMES) AND ITS RELATIONSHIP TO THE BIRDS' BIOLOGY. By Robert W. Storer. Miscellaneous Publications, no. 188, Museum of Zoology, University of Michigan. 2000: 90 pp. ISBN: 9991895418. \$27.00 (paper).—THE METAZOAN PARASITE FAUNA OF LOONS (AVES: GAVIIFORMES), ITS RELATIONSHIP TO THE BIRDS' EVOLUTIONARY HISTORY AND BIOLOGY, AND A COMPARISON WITH THE PARASITE FAUNA OF GREBES. By Robert W. Storer. Miscellaneous Publications, no. 191, Museum of Zoology, University of Michigan. 2002. 44 pp. \$13.20 (paper).—Are you tired of the narrow-standard articles that clog ornithological journals? Are you eager for new ideas from a natural historian who takes a refreshing and broader look at avian biology? If so, read Robert W. Storer's masterly twin monographs on the parasites of loons and grebes, two often-associated groups of waterbirds whose ancestry and relationship have long been controversial.

To be sure, most ornithologists will skip over the "Results" of these papers, which include (1) the dry documentation of the internal (digenetic trematodes, tapeworms [cestodes], spiny-headed worms [acanthocephalans], round worms [nematodes]) and external (leeches, mites, lice) parasites that have been reported living in or on each species of grebe and loon; (2) a list of known prey species and indications of their prominence in the diet (for food is the source of the infecting internal parasite and the numerical abundance of an intermediate host species determines the chances of becoming infected); and (3) brief tutorials on the biology of parasites and examples of the life cycles of some important forms.

These papers would be important enough (if unexciting) contributions if they consisted only of documentation, analysis, and review of the literature on parasites in these two groups. But they cover much more. Storer transcends the facts of who parasitizes whom

and continues with broad-ranging reflections in which he distills a lifetime of thought about paleontology, anatomy, and natural history to consider how knowledge of parasites bears on understanding the evolution of loons and grebes. His "Discussion" centers on how the biology of the bird species relates to their parasite faunas, and vice versa, and the routes taken to investigate this. For example—how does a bird's morphology affect the parasites it acquires? Bill shape and size is related to differences in size and/or species of prey, which affects the relative number of different intermediate hosts taken. This is also related to maneuverability. Foot shape (including presence or absence of a muscle that flexes the second toe) is related to underwater maneuverability, allowing rapid pursuit of fish or constraining the bird to feeding from the bottom. The difference in prey results in different parasites.

The grebes' unique habit of feather eating helps them to cast pellets, which reduces a parasite's chances of setting up house in the upper digestive tract. The feather mat may keep some parasites from reaching the lower tract. As lost feathers need to be replaced, it appears that the continual molt in some tracts is related to the challenge of being parasitized.

Habitat has a major effect on parasites. Both loons and grebes have a totally aquatic life, but some move from fresh to salt water seasonally. Salt water may get rid of fresh water parasites but replace them with species from salt water prey.

If the biology of the bird is important, what about the biology of the parasites? The numbers and kinds of intermediate hosts play a role in determining the kinds of organisms that can be the definitive host. Unfortunately, we are woefully ignorant about the biology of parasites. Life cycles have been worked out for fewer than half the species of helminths reported from grebes. Of nematodes, 38 species are known to parasitize grebes; 9 of these species are considered to be grebe specialists,

yet 3 are known only from the original descriptions.

Despite sharing common habitats or localities for much of the year, loons and grebes harbor different parasite faunas, which reflect different histories. Storer reviews paleontological, geological, and biological evidence that bears on the history of the two groups and argues that it is time to speculate on origins, noting that "the best analyses of the evolution of any group of organisms are those based on the broadest range of supporting evidence." This includes parasitology, which most avian taxonomists give short shrift. His general conclusion is that loons developed from aquatic marine birds in the Northern Hemisphere and that grebes probably originated from marsh dwelling predecessors in South America or Antarctica (not Australia). The basis for his thinking (in Loon parasites, pp. 16–21) is required reading for anyone considering the ancestry of these groups—and even for those who may have pondered why grebes have lobed toes. His list of priorities for future work will keep students busy for decades. On a broader, but parallel topic, he pleads for museums and universities to teach basic whole-animal biology, and bemoans students who "learn to make cladistic analysis before they know the basic biology of the organisms that they are analyzing."

Storer has played a major role as researcher and teacher in North American ornithology in the 20th century, and kicks off his 8th decade of refereed papers and the 21st century with a major accomplishment. These two works represent a synthesis and distillation of information from a lifetime of scholarship. They are memoirs in the true sense of the word, and they challenge us to peek behind a door hiding parasites—a door that most of us have left closed. We recommend these volumes not because of the information about parasites but because they show what one needs to think about when studying birds.

We congratulate the author and the Museum of Zoology at The University of Michigan for publishing ideas that would never appear in the journals and that will stimulate renewed thinking about the early evolution of these birds.—RICHARD C. BANKS and JOSEPH R. JEHL, JR., National Museum of Natural

History, Washington, D.C.; e-mail: banksr@si.edu and grebe5k@cs.com

**THE BOWERBIRDS:** Ptilonorhynchidae. By Clifford B. Frith and Dawn W. Frith, illustrations by Eustace Barnes. Oxford University Press, New York, 2004: 508 pp., 8 color plates, 38 tables, 82 figures, 20 range maps. ISBN: 0198548443. \$164.50 (cloth).—This 10th volume in Oxford University Press' *Bird Families of the World* monograph series continues the tradition of excellence established in previous volumes. It is written by two of the world's leading bowerbird biologists. They co-authored 41 of the 1,048 references cited in the volume, and one or the other was first author on an additional 20. They undertook a world study tour of major institutional collections to gather unpublished and widely scattered information about the biology of this fascinating family of birds. As a result of their labors, they have produced an exhaustive study that will likely be the standard reference on the Ptilonorhynchidae for decades.

Bowerbirds have long been of interest to biologists. The family includes both monogamous and polygynous species, some species of the latter showing pronounced plumage dimorphism, species of the former being largely monomorphic. They have proportionally larger brains than ecologically similar passerines, suggesting high intelligence. Males of some species build elaborate bowers, artistically decorated with colorful feathers, flowers, fruits, shells, bones, and a bewildering assortment of natural and man-made objects. Some manufacture paint and paint their bowers with plant-matter brushes. Like the birds-of-paradise, elevation in the rugged mountains of New Guinea may be the most important sorting mechanism that has facilitated adaptive radiation in the family. Whether your interests are in sexual selection, adaptive radiation, foraging ecology, or anything else, the bowerbirds have something to offer.

The book is divided into two parts, the first consisting of seven thematic chapters, and the second consisting of family, genus, and species accounts. Taxonomically, the authors treat the bowerbirds as a monophyletic family of 8 genera, 20 species, and 23 additional subspe-

cies. All are confined to Australasia, with 12 species found in New Guinea and associated islands (10 endemic) and 10 found in Australia (8 endemic). The 1st chapter is an introduction to the bowerbirds that highlights the long history of human interaction with them. Chapter 2 deals with systematics and biogeography, including the history of taxonomically grouping the bowerbirds in the same family with the birds-of-paradise and the present view that the two groups belong in separate families that are not as closely related as previously thought. Chapter 3 deals with foraging and other behaviors and ecological cycles. Chapter 4 covers morphology, plumages, demography, bower sites, and the four types of bowers—"court," "mat," "avenue," "maypole"—and their significance. The 5th chapter focuses on bower site acquisition—including courtship displays—and fidelity, and the 6th focuses on breeding biology and parental care. Chapter 7 is a treatment of the evolution of mating systems and the role of sexual selection. The first 7 chapters occupy 222 pages; some of the information in these chapters is redundant compared with information provided in the species accounts, but the redundancy was necessary for making comparisons and syntheses. Chapter 8, the second part of the book, consists of the family, genus, and species accounts, and occupies 214 pages. Each species account follows a format that usually includes the following sections: an introduction to the species (a thumb-nail sketch); description, including plumage and color; distribution; systematics, nomenclature, subspecies (if any), and measurements; habitats and habits; diet and foraging; vocalizations and other sounds; mating system; bower sites and bowers; bower site attendance and activities; courtship behavior; breeding; survival and longevity; annual cycle; status and conservation; knowledge gaps and research priorities; and aviculture. A range map for each species also includes the distributions of subspecies. For many species, spectrograms are included as well as photographs and line-drawings. The first color plate consists of six photographs of males at their bowers, and the second portrays six of females at their nests. Plates 3–8 illustrate the 20 species, including the male and female of sexually dimorphic species, subspecies where plumage differenc-

es are pronounced, a few juveniles, and several intermediate plumages. The quality of the plates is uniformly excellent—beautiful paintings of beautiful birds. The book concludes with two appendices, the first a summary of plant species eaten by Australian bowerbirds, and the second a summary of the animal component of adult and nestling diets of 13 bowerbird species, followed by a glossary, a bibliography, and an index.

A. J. Marshall, a great student of bowerbirds, considered bowerbirds the most interesting of the 144 families of birds with respect to behavioral complexity. Many would agree with him, and this book brings together and organizes virtually all that is known about this interesting family of birds. It is well-written, well-organized, and beautifully illustrated. There is much that is not known about bowerbirds, and, in the long run, the heuristic value of this book may be crucial to increasing our knowledge about bowerbirds. I have observed 14 species of bowerbirds in the wild, and reading this book has enhanced my interest in that fascinating family of birds. It is an expensive book, but it is worth the price. I highly recommend it.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

BIOMETRICS OF BIRDS THROUGHOUT THE GREATER CARIBBEAN BASIN. By Wayne J. Arendt, John Faaborg, George E. Wallace, and Orlando H. Garrido. Proceedings of the Western Foundation of Vertebrate Zoology, Volume 8, Number 1. 2004: 33 pp. plus a CD-ROM. ISSN: 05117550. \$25.00 (paper).—The avifauna of the Caribbean Islands have prompted a large number of groundbreaking studies in such diverse areas as biogeography (Ricklefs and Cox 1972), community structure (Case et al. 1983, Faaborg 1985), parasitology (Fallon et al. 2004), and the ecology of overwintering migrants (Faaborg et al. 1984, Holmes et al. 1989, Marra et al. 1998). With the rise of DNA-based studies and molecular phylogenies, some people may harbor the notion that ornithological studies based in biometrics are a thing of the past. But with the present contribution of a massive data set on the biometrics of birds of the Caribbean

Basin from Wayne Arendt and co-authors, the Caribbean Islands continue to offer possibilities for new and revealing analyses of avian ecology and evolution.

Based on the measurement of almost 30,000 individual live birds of 276 species captured with mist nets, this publication presents morphological measurements for as many as nine characters, including body mass, and lengths of the wing chord, penultimate primary, tarsus, central rectrix, exposed culmen, culmen from the nares, and culmen depth and width. In addition, age and sex of each individual were recorded when known. While many of the data are from Puerto Rico, a total of 30 islands are represented, with significant samples from Cuba and the Dominican Republic, as well as many smaller islands traditionally less-studied by ornithologists.

The printed portion of this short publication begins with a preface containing a history of this compilation of avian biometrics and a summary of the many sources of data gathered here. There follows a somewhat out-of-place section on the uses of morphological data, including an extensive listing of representative works in avian genetics and evolution, energetics, age and sex determination, ecomorphology, conservation and management, biogeography, and population and community ecology. While this section serves well as a ready source of references to biometric-based studies, it more rightly belongs in the introduction and/or discussion sections, where much of the same material is repeated.

Following the preface, the authors present a short introduction, wherein the importance of morphological measures to various subdisciplines of ornithology is reiterated and other sources of mensural data are detailed. The focus is appropriately placed on the outstanding need for body mass, and especially appendicular measurements, of Caribbean birds. Study areas are briefly described, and methods of obtaining measurements are detailed, though these are by now fairly standardized. Most important is a section explaining how to read the "Morphometrics Table" and the individual files for each species, all of which are presented on the CD that accompanies this volume. Analyses and results are limited to the descriptive statistics of mean, standard deviation, and range for body mass and longitu-

dinal measurements. The discussion again reiterates the potential value of biometric data and concludes with the authors' statement that they hope this publication will "serve as a tool for future researchers to use in their studies in the West Indies and throughout the Greater Caribbean Basin to better explain the morphological variation among the birds." The literature cited section contains a useful bibliography of nearly 300 references, many of which are examples of how avian biometrics data have been used.

The heart of this publication is undoubtedly found in the accompanying CD, which contains all of the raw data as well as summary statistics for 30,000 individuals. Species are presented in phylogenetic order, and then grouped by island, age, and sex, so that subsets of these data are easily extracted. Descriptive statistics and sample sizes are presented for the species as a whole, and for each island, with separate statistics by age and sex (when known). These statistics are found at the end of the species-specific tables, but are more easily accessible and summarized in the single "Morphometric Table" for all species. Species-specific data can be found in this table, or through a convenient index of species names. Although this index presents only Latin names, this should be a minor inconvenience to only the occasional user.

Negative criticisms of this work are few. A convenient summary of banding sites and vegetation associations is printed as a table, but I think these site descriptions could be significantly enhanced by adding latitude and longitude coordinates or other locational information so that the reader may determine more precisely where sites are found. In addition, descriptions of vegetation associations are very basic (i.e., wet, dry, mesic, dwarf), and would be more valuable if more detailed. I found few problems with the text, although in two places the authors attempt incorrectly to identify species to the subspecific level. The Sharp-shinned Hawk is identified as *Accipiter striatus venator* on all islands, which is the form found only on Puerto Rico; other forms are resident on Hispaniola (*A. s. striatus*) and Cuba (*A. s. fringilloides*). Similarly, the Palm Warbler (*Dendroica palmarum*) is misidentified as the Yellow Palm Warbler on all islands. The Yellow Palm Warbler (*D. p.*

*hypochrysea*) occurs in the West Indies, but is far less abundant than the Western Palm Warbler (*D. p. palmarum*).

Finally, while this publication may be criticized for its lack of in-depth analyses, that task would be monumental; the potential applications and uses of the data as presented are enormous. Rather than jealously guarding the data, these authors and their collaborators are to be congratulated for sharing the raw data so that we all might join in the fun and benefit from its use. Publication of this data set is also likely to spur the emergence of additional data. As the authors point out, 30,000 birds is a large number, but once samples are divided by species, age, sex, and island, sample sizes can diminish quite rapidly, especially for the least common species. Additional data may be required for meaningful analyses of variation in biometrics of many of these species, and many of the most interesting endemics are not represented at all.

Nevertheless, alongside the Western Foundation of Vertebrate Zoology's publication of a bibliography of ornithology in the West Indies (Wiley 2000), this monumental work of biometric data represents a significant advance in Caribbean ornithology. Although not intended for popular consumption, the work should find a place in the collections and databases of researchers interested in avian systematics and evolution, morphology and ecomorphology, avian biogeography and ecology in general, and Caribbean ornithology in particular.—STEVEN C. LATTA, PRBO Conservation Science, Stinson Beach, California; e-mail: slatta@prbo.org

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**BIRDS OF ECUADOR.** By Niels Krabbe and Jonas Nilsson. Bird Songs International BV, Netherlands. 2004. DVD-ROM for Windows 98, ME, 2000, XP.—This DVD is a compendium of 6,015 individual recordings of 1,184 species, and 824 photographs of 469 species. Learning bird vocalizations greatly enhances the number of species that can be detected on almost any birding trip, but is especially important in the tropics. It can be difficult to find recordings that cover even the common species for most of the Southern Hemisphere, and comparing vocalizations can be a frustrating experience. This DVD brings vocalizations of nearly all of Ecuador's birds together to aid in learning and comparing vocalizations.

This DVD uses modern technology to great advantage by placing the vocalizations of the vast majority of Ecuadorian birds on your computer and at your fingertips. The DVD is organized taxonomically by family. Clicking on a family brings up a species list with icons that indicate whether a photograph or sound track is available for a given species. Clicking on the species brings up a small image of the photograph (if available) and lists the sound recordings available. For some species, there is information on taxonomy or recent splits. Many recordings may be available for each species, and if appropriate, they are separated by subspecies. Information under the sound bar for each selection includes a rating of the quality of the recording, the type of vocalization (song, call, duet, etc.) and whether the vocalization was recorded under natural conditions or after playback. Yet another click on the twistee under the sound bar brings up complete information on the recording, in-

cluding the recordist, location, date, time of day, archive or reference information, and often the identification of other species heard in the recording. The location where it was recorded is a clickable link that takes you to two maps showing Ecuador and South America, with the recording location indicated by a dot on the maps.

I had no trouble using the "Playlist" feature to create playlists for various geographical regions of Ecuador. Creating a playlist involves dragging and dropping recordings to the list. Playing the list requires one click. As the list is played, the species' twitree opens, showing all recordings on the list for that species, and, as each recording is played, the information on that cut is displayed. Once a playlist is created, the program will build a folder of the selections that may be copied to other media for use in whatever software the owner has on their computer. Again, this is straightforward, and creating the folder to use for burning a CD is easy.

The recordings are variable in quality (good to excellent), and, as most are unfiltered, there is background noise of microphones, rain, and other (unidentified) animals. Some of the cuts contain human speech or other sounds (a Spanish radio station, for example). To me, it is preferable to have these intrusions than to have them cut out of the recording (changing the time between vocalizations) or filtered out (altering the recording). The first time I came across a snippet of Dutch on a recording it made me feel as though I was in the field with Krabbe and Nilsson, and their excitement was palpable, adding to the experience of listening to the recording and not detracting from it.

Not all recordings are identified with 100% certainty. When there is any doubt as to the species represented, there is a notation under the sound bar with a percent certainty rating from 50 to 99%. While it is always preferable to have recordings of known bird origin, some

species do not vocalize where they can be seen. As long as the uncertainty is identified (as it is here), to me it is better to have a 99% certainty in identity than to have a blank in the species list or the variation in vocalizations left unrepresented.

The photographs are also variable in quality. I have to admit, I would not buy the DVD for the photographs alone. They are a welcome addition to the whole, and some are truly fantastic, including an admittedly somewhat fuzzy photograph of a recently described Jocotoco Antpitta (*Grallaria ridgelyi*) in the wild. Many photos depict birds in hand, some head studies, and some of the entire bird. Using the slide show feature, full-screen shots of the birds are shown on the computer screen and change at the selected time interval. The species, subspecies, scientific name, and photographer are displayed in a narrow bar on the top, and four icons at the bottom allow you to browse forward or backward through the slideshow; they provide information on the date and place the photograph was taken and contact information for the photographer.

The DVD may be installed in English or Spanish versions. There is a useful errata page on the Web, with a patch that allows users to "see" an otherwise unavailable species. The DVD was easy to load on both a desktop PC and a laptop, and its use and playlists were easily created using the Help feature the first time; those needing assistance will find contact information for Help in the "read me" documentation. This "read me" note also includes important information on how the recordings were edited, and it includes the acknowledgments. This product includes 69 hours of vocalizations of the birds of Ecuador. It will be extremely useful to field biologists and birders who want to learn the vocalizations of these species. This DVD is highly recommended.—MARY GUSTAFSON, Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: mary\_gustafson@usgs.gov

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## THE WILSON BULLETIN

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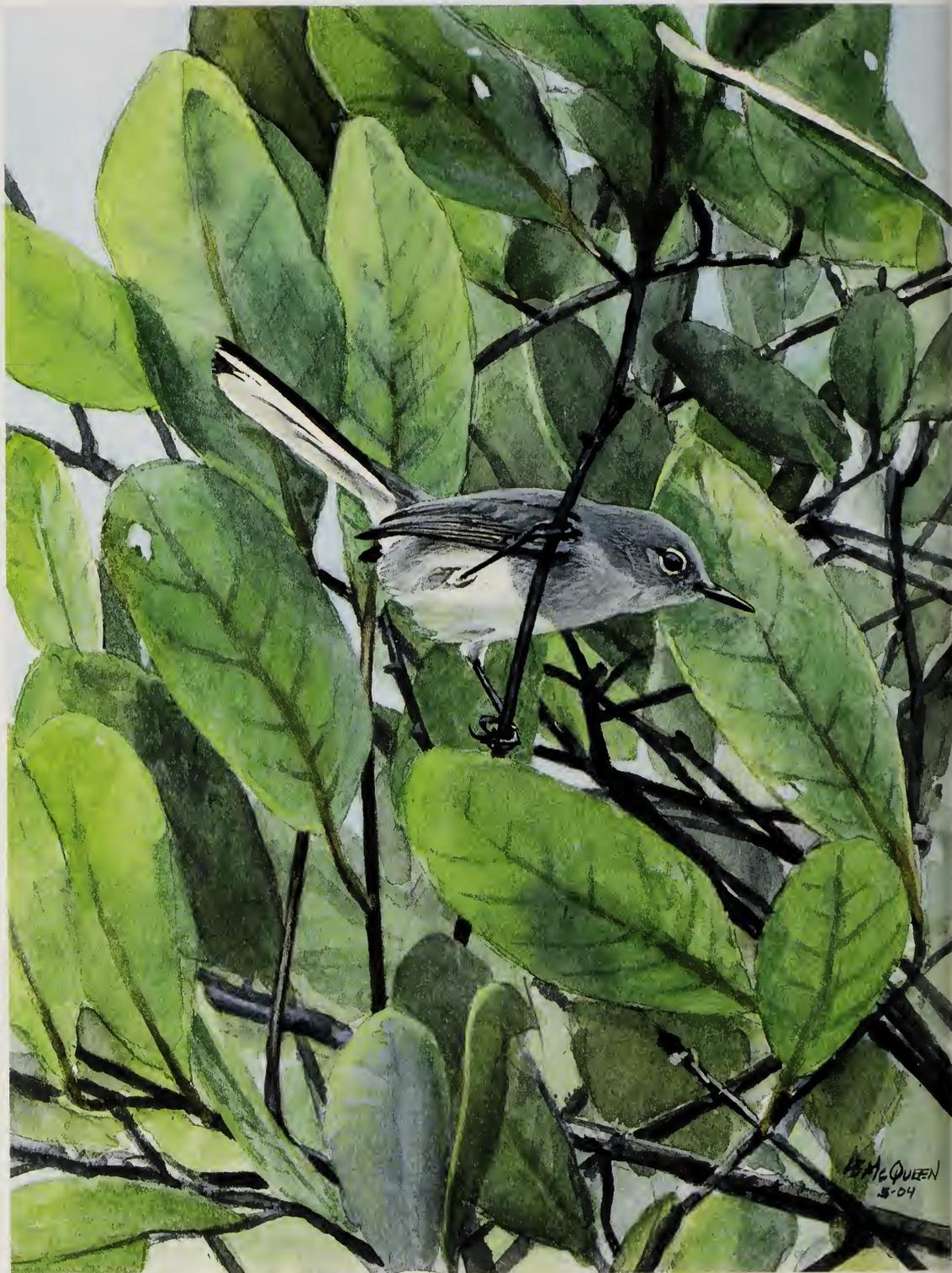
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FRONTISPIECE. Iquitos Gnatcatcher (*Polioptila clementsi* sp. nov.), the fourth new bird species described from the Reserva Nacional Allpahuayo-Mishana near Iquitos, Peru since 1998; tree is *Caraipa tereticaulis* (Clusiaceae). Original watercolor painting by Lawrence B. McQueen.

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## A NEW SPECIES OF GNATCATCHER FROM WHITE-SAND FORESTS OF NORTHERN AMAZONIAN PERU WITH REVISION OF THE *POLIOPTILA GUIANENSIS* COMPLEX

BRET M. WHITNEY<sup>1,3</sup> AND JOSE ALVAREZ ALONSO<sup>2</sup>

**ABSTRACT.**—We describe a new species of gnatcatcher, *Polioptila clementsi*, from white-sand (*varillal*) forest at the Allpahuayo-Mishana National Reserve, about 25 km by road west of Iquitos, Peru. To date, the new species is known only from the reserve, and is rare even there. Comparisons of morphological and vocal characters confirm that it is a member of the *Polioptila guianensis* complex, which comprises at least three poorly known, allopatric taxa ranging from the Guianas and the Rio Negro region through much of Amazonia south of the Amazon River. Roughly equivalent levels of phenotypic differentiation are documented for all taxa east of the Andes, including the new species. In consideration of the fact that some other species complexes in the genus comprise sister taxa showing lower levels of phenotypic differentiation, both morphologically and vocally, we recommend that *Polioptila guianensis*, *P. facilis*, and *P. paraensis* henceforth be recognized as separate species. *Received 4 June 2004, accepted 1 March 2005.*

**RESUMEN.**—Describimos una nueva especie de perlitita, *Polioptila clementsi*, del bosque de arena blanca (*varillal*) de la Reserva Nacional Allpahuayo-Mishana, a 25 km por carretera al oeste de Iquitos, Perú. Hasta la fecha, la nueva especie es conocida solamente de la reserva, y es rara incluso allí. Comparaciones de caracteres morfológicos y vocales confirman que es un miembro del complejo *Polioptila guianensis*, que comprende al menos tres taxones alopatricos muy poco conocidos, que se extienden desde la región de las Guayanas y el Rio Negro a través de gran parte de la Amazonía al sur del Rio Amazonas. Son documentados niveles aproximadamente equivalentes de diferenciación fenotípica para todos los taxones al este de los Andes, incluyendo la nueva especie. En consideración al hecho de que algunos otros complejos de especies en el género comprenden taxones hermanos que muestran una diferenciación fenotípica menos marcada, tanto morfológica como vocal, recomendamos que de aquí en adelante *Polioptila guianensis*, *P. facilis*, y *P. paraensis* sean reconocidas como especies separadas.

The recent discovery of two species of birds new to science (Ancient Antwren, *Herp-silochmus gentryi* and Allpahuayo Antbird, *Percnostola arenarum*) and several others previously unknown from Peru in the white-sand forests of northern Loreto has revealed the presence of an avifauna with close Guianan

affinities extending westward from the Iquitos area into eastern Ecuador (Alvarez and Whitney 2003). In the early stages of recognizing this pattern, we focused fieldwork on searches for additional species we predicted to have a high likelihood of occurrence in the various white-sand forest types in this region. Among these was *Polioptila guianensis* (Guianan Gnatcatcher), a poorly known canopy insectivore represented by about 30 specimens in the world. Its nearest documented point of occurrence lay some 800 km distant along the upper Rio Negro in Brazil near São Gabriel da Cachoeira (BMW pers. obs.).

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On 9 September 1997, JAA found what appeared to be *Poliioptila guianensis* in tall, white-sand forest in the proposed Allpahuayo-Mishana Reserve outside Iquitos on the road to Nauta. He noted, however, that the birds' songs differed distinctly from BMW's recordings from Brazil. In subsequent years, we obtained three specimens and a good sample of recordings of the songs and calls of this gnatcatcher, which appears to have a highly restricted distribution, even within the reserve. After comparing our specimens and sound recordings with those of all Neotropical gnatcatcher species, especially *P. guianensis* from diverse points in its distribution, we are convinced that the Iquitos-area birds are most closely related to *P. guianensis*, and would best be described as a new species, which we propose to name:

*Poliioptila clementsii* sp. nov.

Iquitos Gnatcatcher

Perlita de Iquitos

*Holotype*.—Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru, No. 21113; male (skull unossified) from the Zona Reservada Allpahuayo-Mishana, 03° 55' S, 73° 29' W, south bank of Rio Nanay, approximately 25 km wsw of Iquitos, Department of Loreto, Peru; 150 m elevation; 15 December 1998; collected by JAA. Voice specimen of an accompanying individual is archived at the Macaulay Library of Natural Sounds (MLNS), Cornell Laboratory of Ornithology, Ithaca, New York; LNS 120444. A sample of liver tissue was preserved (Alvarez No. 1.12.98) and will be accessioned at the Louisiana State University Museum of Natural Science (LSUMZ) once it is legally exported from Peru.

*Diagnosis of Poliioptila clementsii* sp. nov.—A typical member of *Poliioptila* (*sensu* Ridgway 1904:710–711), including a thin black bill and graduated tail, with narrow rectrices bearing conspicuous white on the outer three pairs but none on the three central pairs. The following pertains only to males, as we have no specimens of female *P. clementsii*. Readily distinguished from all congeners except *P. guianensis*, from which it differs by its significantly longer bill (mean 12.1 versus 11.4 mm; culmen from base at skull). On a taxon-

by-taxon basis, differs from *P. g. guianensis* by uniformly gray throat and breast (instead of throat conspicuously paler than breast) and presence of black bases on outer and penultimate pairs of rectrices, with third pair mostly black (instead of three outer pairs entirely, or almost entirely, white); from *P. g. facilis* by presence of a conspicuous, broken white eye-ring (lacking in *P. g. facilis*) and greater extent of white on outer rectrices (approximately basal 1/3–1/2 black in *P. g. facilis*); from *P. g. paraensis* by generally darker and more bluish-gray plumage, and greater extent of white on outer rectrices (approximately basal 1/3–1/2 black in *P. g. paraensis*). Readily distinguished from *P. schistaceigula*, the purported closest relative of *P. guianensis* (Zimmer 1942), by much paler plumage overall and somewhat longer tail with extensive white (rectrices essentially all black in male *P. schistaceigula*). Males of all other species of *Poliioptila* have discrete areas of black on the head (ranging from streaks to extensive caps) in definitive alternate plumage, among other differences.

*Diagnosis of voice*.—Loudsong structurally similar to, but immediately distinguished from, all forms of *P. guianensis* by presence of sharp, “inverted chevron-shaped” introductory notes (virtually always three of these) delivered slowly enough to be counted in the field, followed by a series of evenly spaced notes delivered at a faster pace than by any of the taxa of *P. guianensis*. The loudsong of *P. schistaceigula* is a variable set of notes lacking coherent, repetitive structure in series, and is thus very different; other species of Neotropical gnatcatchers are widely and variably divergent in both songs and calls.

*Distribution*.—Known only from tall, *Carai-pa*-dominated *varillal* forest (see Habitat and behavior section below) at the type locality (the Reserva Nacional Allpahuayo-Mishana) just west of Iquitos, Department of Loreto, Peru.

*Description of holotype*.—See color frontispiece. Capitalized color designations (corresponding number in parentheses) from Smithe (1975). Rictal bristles present, inconspicuous. Upperparts from base of bill to uppertail coverts, sides of head, and upperwing coverts essentially uniform and closest to Dark Neutral Gray (83), in some lights appearing slightly more bluish, toward Plumbeous (78). Head

lacking discrete areas of black or white except for a narrow, white eye-ring, slightly broken at front and back edges. Throat and breast, including some posterior extension to sides, slightly paler than upperparts (lightest at the lower breast/upper belly), Medium to Light Neutral Gray (84–85). Belly and undertail coverts white. Primaries and secondaries closest to Blackish Neutral Gray (82), outer vanes of primaries finely edged with same gray as upperparts, inner vanes narrowly edged whitish. Alula and smaller, overlying feather blackish with thin whitish margin on outer vane; primary coverts same blackish but lacking whitish margins. Underwing coverts white, the tiny coverts at base of outer primaries and at bend of wing with dark gray centers and whitish tips. Tail full (12 complete rectrices) and unabraded, distinctly graduated. Three inner pairs entirely blackish. Black/white pattern on No. 4 and No. 5 differs on left and right sides of the bird, the right side having somewhat more white, especially on the outer vanes. Rectrix No. 4 mostly blackish with white tip (about 5 mm on inner vanes, to about 10 mm on outer vanes); No. 5 mostly white with approximately basal 1/4–1/3 blackish, on the inner vane extending posteriorly from the rachis to the feather margin in a diagonal strip to invade the white region to within about 15 mm of the tip on the right feather and to within 12 mm of the tip on the left feather. Outer rectrices (pair No. 6) white with about basal 1/5 of outer vane blackish, basal 1/3 of inner vane blackish and showing same diagonal, posterior extension described for No. 5 only to a lesser degree. Rectrices show same pattern on ventral and dorsal surfaces except that No. 4 appears wholly blackish (like the two central pairs, no white tip visible) when viewed from above. Soft parts in life: iris brown, maxilla black with paler commissure, mandible grayish-horn, legs and feet bluish-gray, soles of feet whitish. MUSM 21113 was selected for the holotype because it is in the best condition of the three available specimens, and has a complete and fully grown tail. Its cranium was clear and unossified; thus, it may be a juvenile.

*Measurements of holotype.*—Wing (chord) 45.4 mm, tail 45.8 mm, culmen from base (at skull) 12.7 mm, bill width at anterior edge of nares 2.3 mm, tarsus 15.3 mm, mass 6.0 g.

*Specimens examined.*—Only specimens that were measured are listed. Specimens of all other *Polioptila* species in South America were compared superficially. The sample below was restricted to *P. guianensis* and *P. schistaceigula*, the presumed closest relatives of *P. clements*. Some standard measurements of these specimens, with sample sizes, are presented in Table 1.

*Polioptila clements* sp. nov.: Peru: Loreto, Allpahuayo-Mishana area, three males (MUSM 21111, 21112, 21113).

*Polioptila guianensis guianensis* (eight males, four females): French Guiana: Tama-noir, Mana River, two males (Carnegie Museum of Natural History [CM] 61912, 61923, paratypes); Oyapock, Pied Saut, three males, one female (CM 64921, 65782, 65783; American Museum of Natural History [AMNH] 233949, paratypes). Suriname: Maroni District, Negerkreek, one female (AMNH 461499). Guyana: Potaro Landing, one female (AMNH 126034); Iwokrama Forest Reserve, one male, one female (Academy of Natural Sciences [ANSP] 188049, 188050). Brazil: Amazonas, north of Manaus, two males (Museu Paraense Emílio Goeldi [MPEG] 53260, 53261).

*Polioptila guianensis facilis* (five males, one female): Venezuela: Amazonas, Solano, one male (AMNH 433542, holotype); Mt. Duida, Rio Pescado, one male (AMNH 275037, paratype). Brazil: Amazonas, Mt. Curucuryari, one female (AMNH 311254, paratype); Parque Nacional do Jaú, two males (MPEG 50678, 50679); Roraima, Colônia do Apiaú, one male (Field Museum of Natural History [FMNH] 344215).

*Polioptila guianensis paraensis* (two males, three females, one sex unknown): Brazil: Pará, Município Capim, one male, one female (Museu de Zoologia da Universidade de São Paulo [MZUSP] 45687, 45693); Caxiricatuba, one male, one female (AMNH 287648, 287649); Amazonas, Borba, Rio Mapiá Grande, one sex unknown (MPEG 53263); Rondônia, Cachoeira Nazaré, one female (FMNH 344216).

*Polioptila schistaceigula* (one male, three females): Colombia: Cauca, two females (AMNH 107540, 133935). Ecuador: Esmeraldas, Cachabí, one male (AMNH 502979, holotype); Pichincha, one female (LSUMZ 162122).

TABLE 1. Some standard measurements of *Poliophtila clementsii* sp. nov., *P. guianensis* (three subspecies), and *P. schistaceigula* from northern South America. Values are means (range, n).

Taxon	Bill width (mm) <sup>a</sup>	Culmen (mm) <sup>b</sup>	Wing chord (mm) <sup>c</sup>	Tail (mm)	Body mass (g)
<i>P. clementsii</i>					
Male	2.4 (2.3–2.5, 3)	12.1 (11.7–12.7, 3)	44.3 (43.5–45.4, 3)	46.6 (45.8–47.6, 3)	5.6 (5.1–6.0, 3)
<i>P. g. guianensis</i>					
Male	2.3 (2.2–2.5, 8)	11.5 (10.9–12.0, 6)	46.6 (44.5–49.0, 8)	46.5 (44.1–48.9, 4)	6.2 (5.4–6.9, 3)
Female	2.4 (2.3–2.4, 2)	11.4 (11.1–11.6, 3)	46.0 (45.5–46.6, 2)	43.9 (1)	6.0 (1)
<i>P. g. facilis</i>					
Male	2.5 (2.3–2.7, 5)	11.4 (11.1–11.7, 5)	45.3 (44.8–45.7, 5)	46.3 (45.2–47.4, 5)	5.9 (5.5–6.5, 3)
Female	—	11.8 (1)	44.2 (1)	46.3 (1)	—
<i>P. g. paraensis</i>					
Male	2.5 (1)	12.0 (11.9–12.0, 2)	45.0 (44.5–45.5, 2)	50.3 (48.8–51.8, 2)	—
Female	2.5 (2.3–2.7, 2)	11.4 (10.8–11.9, 3)	45.5 (43.0–49.0, 3)	48.6 (47.2–50.1, 3)	5.8 (1)
Sex unknown	2.5 (1)	10.8 (1)	43.0 (1)	48.9 (1)	5.9 (1)
<i>P. schistaceigula</i>					
Male	2.5 (1)	13.7 (1)	46.9 (1)	42.4 (1)	—
Female	2.5 (2.4–2.5, 3)	12.3 (11.9–12.7, 3)	44.4 (43.7–45.6, 3)	41.6 (38.6–43.4, 3)	6.0 (1)

<sup>a</sup> Measured at anterior edge of nares.<sup>b</sup> Measured from base at skull.<sup>c</sup> Both wings usually measured; longer measurement included here.

*Tape recordings examined.*—Sample sizes are number of individuals recorded; 1–4 vocalizations of each type were measured for each individual (means and ranges for samples are presented in Table 2). *Poliophtila clementsii* sp. nov.: Peru: Loreto, Allpahuayo-Mishana area, 10 loudsong (9 JAA, 1 BMW), 8 calls (7 JAA, 1 BMW). *Poliophtila guianensis guianensis*: Brazil: Amazonas, north of Manaus, two loudsong, two calls (all L. Naka). *Poliophtila guianensis facilis*: Brazil: Amazonas, near São Gabriel da Cachoeira, seven loudsong (4 BMW, 3 K. J. Zimmer), four calls (K. J. Zimmer). *Poliophtila guianensis paraensis*: Brazil: Pará, Caxiuanã National

Forest, six loudsong (5 BMW, 1 C. A. Marantz); Serra dos Carajás, two loudsong, one call (all BMW); Novo Progresso, one loudsong (J. F. Pacheco); Vila Braga, one loudsong (BMW); Jacareacanga, one loudsong (BMW); Amazonas, Rio Sucundurí, one loudsong (BMW); Mato Grosso, Comodoro, one loudsong, four calls (A. Whittaker). Two of the *P. clementsii* were collected subsequent to tape recording (the third specimen was in the company of a bird that was tape recorded); none of the *P. guianensis* was collected.

*Biochemical specimens.*—Tissues were saved in DMSO (dimethylsulfoxide) buffer solution (to be deposited at LSUMZ once it is

TABLE 2. Some measurements of *Poliophtila clementsii* and *P. guianensis* (three subspecies) loudsongs from northern South America. Values are means (range; no. of vocalizations, no. of individuals).<sup>a</sup>

Taxon	Pace of first three notes	Pace without first three notes	$\Delta PF^b$
<i>P. clementsii</i>	0.14 (0.13–0.16; 33, 10)	0.07 (0.06–0.07; 33, 10)	1.98 (1.75–2.30; 33, 10)
<i>P. g. guianensis</i> <sup>c</sup>	0.12 (0.12–0.13; 2, 2)	0.14 (0.13–0.15; 2, 2)	0.47 (0.31–0.63; 2, 2)
<i>P. g. facilis</i> <sup>d</sup>	0.08 (0.07–0.10; 20, 6)	0.13 (0.12–0.14; 19, 6)	0.94 (0.52–2.33; 20, 6)
<i>P. g. paraensis</i> <sup>e</sup>	0.09 (0.07–0.10; 15, 6)	0.11 (0.09–0.12; 15, 6)	0.37 (0.21–0.61; 15, 6)

<sup>a</sup> Means and ranges reflect combined measures of the number of birds recorded. All measurements taken at peaks of notes.<sup>b</sup> Change in peak frequency from first to last note.<sup>c</sup> Sample from near Manaus, Amazonas, Brazil.<sup>d</sup> Sample includes both banks of upper Rio Negro, Amazonas, Brazil.<sup>e</sup> Sample from Caxiuanã National Forest, Pará, Brazil.

exported from Peru) for all three of the specimens of *Poliioptila clementsii*. We know of four tissue samples of other members of the *P. guianensis* complex (see Specimens examined listed above): ANSP 188050 is tissue number ANSP 8192; ANSP 188049 is tissue number ANSP 8307; and MPEG 53260 and 53261 are tissue numbers LSUMZ B-20230 and B-20266, respectively.

*Etymology*.—We are pleased to name this new species in honor of James F. Clements in recognition of his generous and forward-thinking contribution to preserving the Allpahuayo-Mishana National Reserve, and the habitat of *Poliioptila clementsii* in particular. Jim's influence on the world of birding, primarily through his carefully maintained world checklist of birds, has been enormous and has sparked the interest of many birders to travel to remote places in search of rarities like the Iquitos Gnatcatcher. The money generated by the activities of birders has ever-growing importance in supporting local economies, and it encourages government authorities to recognize the economic value of ecosystem preservation.

#### REMARKS

*Variation in the type series*.—The type series consists of the three male specimens listed above, all of which have essentially unossified skulls and are probably juveniles. One of them (MUSM 21111) was one of four individuals foraging together in a mixed-species flock and was thought to have been giving food-begging calls. Plumage of this specimen and MUSM 21112 closely match the description of the holotype. The holotype and MUSM 21111 were collected in mid-December, and both showed contour molt but no molt in the flight feathers. MUSM 21112, taken in early April, also showed contour molt and had half-grown central rectrices with the right outer rectrix barely emergent from its sheath. All specimens show the slight variation in pattern of black and white on the rectrices described for the holotype.

Some variation in iris color can be surmised from the specimen labels. The holotype was "brown," MUSM 21111 was recorded as "grayish-brown," and MUSM 21112 as "pale brown, almost cream." Lacking specimens of adults, it is not possible to comment further

on variability of this feature or other characteristics. Juvenile and other subadult plumages of other *Poliioptila* species are, however, quite similar to adult plumages (these being basic plumages in the cases of species with different alternate plumage; Ridgway 1904, Atwood and Bontrager 2001). This accords well with our sightings from the field. Food-begging birds in the company of singing adults (i.e., the birds feeding them) show no noticeable plumage differences from adults. Furthermore, adults appear to show no plumage variation through the year, never acquiring any conspicuous areas of black or white (e.g., mask, cap) on the head.

*Habitat and behavior*.—*Poliioptila clementsii* appears to be uncommon or rare (encountered 0–3 times per week,  $n = \sim 50$  observations) in the Allpahuayo-Mishana National Reserve, occurring only in white-sand forest having a variable canopy height of about 15–30 m, and is most consistently present in what local botanists have defined as *varillal alto húmedo* (tall, humid *varillal* forest). These physiognomically simple *varillal* forests were characterized by Whitney and Alvarez (1998) and described in detail by García Villacorta et al. (2003). In *varillales*, canopy height and species composition and abundance of plants, even major groups of plants such as bromeliads and palms, varies over a small spatial scale in accordance with edaphic conditions and drainage properties (e.g., Poulsen and Tuomisto 1996, García Villacorta et al. 2003). Similarly, presence of *P. clementsii* is highly patchy and it appears that considerable areas of seemingly suitable habitat contiguous with active territories are not occupied. Since its discovery, careful searches for *P. clementsii* have been conducted in all forest habitats in northern Loreto by using tape recording playbacks and by observing from the ground with binoculars and telescopes; this has enabled us to define its habitat more specifically than has been possible for most other small, forest-based passerines. We had expected to find *P. clementsii* along the middle and upper Rio Nanay. At two places along the upper Nanay, however, we have found *Poliioptila plumbea* (Tropical Gnatcatcher) accompanying mixed-species flocks in the canopy of *varillal* habitats, occupying the potential ecological space of *P. clementsii*. Within Allpahuayo-Mishana,

*P. plumbea* is restricted to seasonally flooded forest along the margins of the Rio Nanay.

Tall trees of *Caraipa tereticaulis* and *C. utilis* (Clusiaceae) are among the dominant canopy trees in appropriate habitat, and pairs or small family groups of *P. clementsi* were often seen foraging in these trees (see frontispiece). Palms (Arecaceae) also occur, including the widespread *Euterpe caatinga* and the less common *Mauritia aculeata* and *M. carana*. Arboreal epiphytes are rare. Understory plant composition is also variable, but is typically dominated by some combination of the ferns *Trichomanes martiusii* and *T. bicornis* (Hymenophyllaceae), the herb *Rapatea ulei* (Rapateaceae), and various species of bromeliads, such as *Guzmania lingulata* and *Neoregelia* sp. (Bromeliaceae).

*Polioptila clementsi* foraged exclusively in the canopy and subcanopy (upper 1/4 of trees) with mixed-species flocks composed primarily of other insectivores and usually including some small frugivores and nectarivores. Attack maneuvers ranged from gleans and short, stabbing reaches to acrobatic chases of fleeing prey as the birds moved lightly and incessantly through the terminal portions of live, leafy branches. All leaf surfaces were checked rapidly. The tail was partially cocked, frequently flicked laterally, and briefly opened slightly to expose the white outer rectrices. (In all these aspects, the foraging behavior of *P. clementsi* appears to be typical for the genus.) These irregular movements may startle small, hidden arthropods into revealing their presence and probably help family members maintain visual contact. The wings were shallowly flicked outward (without opening) almost constantly. This tiny motion may effect a state of readiness for instantaneous pursuit of flushed prey items. Stomach contents of MUSM 21112 contained insect fragments and many small white eggs of an arthropod. One individual that had apparently just bathed was observed sunning itself and preening on a limb for more than 5 min.

**Vocalizations.**—We have documented with tape recordings six types of vocalizations from *Polioptila clementsi*. The loudsong is a distinctly two-parted series of sharp, thin (unmodulated, no harmonics) notes. It begins with three evenly paced (slow enough to be counted in the field) open, “inverted chev-

rons” peaking at approximately 8 kHz, and then breaks into a much faster, trilled series of evenly paced, nearly vertical notes at just over 6 kHz (Fig. 1A). Loudsongs are usually slightly less than 2 sec in duration, but may exceed 2.5 sec after tape-recording playback; no other features have been observed to change following playback of birds’ own songs or songs of other individuals. We analyzed nine loudsong recordings of *P. clementsi*, most of which consisted of 3–20 or more songs. All songs began with the three introductory notes described above; there was no variation in this character. In fact, the loudsong of all individuals was remarkably consistent in all aspects. At least three clearly recorded songs of each individual were extracted and measured using “Canary” 1.2.4 of the Bioacoustics Program of the Cornell Laboratory of Ornithology (Ithaca, New York). Spectrograms were produced using the default settings and 75% overlap.

Although any number of other features could have been quantified, we selected three independent characters for critical measurement: pace (see below) of the first three notes, pace of the rest of the notes (all those after the first three), and change in peak frequency ( $\Delta$ PF) from the first to the last note. Measurements for the three songs from each individual were then averaged to obtain a value that reflected some attempt to control for intra-individual variation (Table 2). All measures were made at the scales shown in Figure 1 and at the peak frequency of notes, as this was the only unambiguous point (i.e., permitting easily reproducible results) on these highly vertically oriented spectrogram traces. The “inverted chevrons” of the first three notes were measured this way, as well, to permit appropriate comparison with the first three notes in the songs of some other taxa in the complex. Thus, pace more effectively quantified the time intervals between notes than the duration of the section measured, because, in the case of the first three notes especially, the measurement point hit not the left/right edges of the open chevrons, but the highest point (peak) of the note. Pace of the first three notes in the loudsong was 0.14 sec (range = 0.13–0.16 sec). Pace of the remaining notes was 0.07 sec (range = 0.06–0.07 sec);  $\Delta$ PF was 1.98 kHz (range = 1.75–2.30 kHz). Both parts of the loudsong

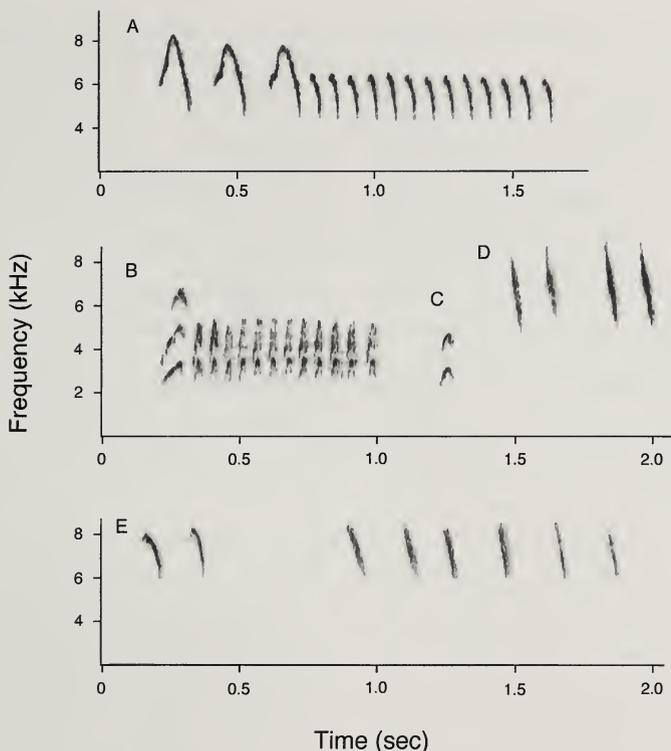


FIG. 1. Sound spectrograms of vocalizations of *Polioptila clementsi*. Recordings are by JAA except as noted. The frequency scale is uniform for all spectrograms, but note that some do not show the area below 4.0 kHz. (A) Typical loudsong showing three distinct introductory notes; all recorded songs were closely similar to this (Table 2); (B) quiet, single-note call with a harmonic heard only a few times; (C) typical multi-note call with emphasis on the introductory note and pronounced harmonics; (D) flight calls, given in doublets (recorded by BMW); (E) irregular series of sharp calls sometimes given while foraging.

were characterized by essentially uniform pace and lack of frequency shifts.

The second most frequently recorded vocalization of *P. clementsi* ( $n = 3$  recordings) was a multi-note call lasting 0.5–1.0 sec, sounding like a brief, quiet chatter, in which the first note is distinctly louder and longer, and all notes have harmonics (Fig. 1B). We have not been able to determine its context. Other vocalizations (represented by only one or two recordings) are a quiet, single-note call having a closed “inverted chevron” shape at about 3 kHz that also has a harmonic (Fig. 1C); a sharp call given in flight that makes a straight, nearly vertical trace from about 5.5 to 9 kHz (Fig. 1D); sharp (bent vertical trace) calls structurally similar to notes in the fast section of the loudsong but peaking at about 8 kHz and often given several times in irregular succession while foraging (Fig. 1E); and a food-begging call similar to the call shown

in E but which features a structurally distinct introductory note ahead of a regularly paced series of sharp notes. One additional vocalization was heard once by BMW, but unfortunately it could not be recorded. A singing bird in the company of its mate responded to playback of its own song by flying out of a tree above the trail (about 12 m above ground) and then tightly circling the narrow canopy of the tree one complete turn (360°) while rapidly pumping its tail up and down as it delivered a distinctively cadenced sound—something like *chik-CHEE-dee, chik-CHEE-dee, chik-CHEE-dee, chik-CHEE-dee*. . . . Such flight displays accompanied by a vocalization quite different from the typical loudsong are occasionally given by many species of oscine passerines (BMW pers. obs.). Their function remains obscure, but in this case the display and vocalization clearly resulted from agita-

tion at the presence of a perceived conspecific male intruder.

*Intragenetic relationships.*—Morphologically, *P. clementsi* is rather weakly differentiated from *P. guianensis*, although it has a longer bill (two-tailed *t*-test,  $P = 0.008$ ), and a diagnostically different tail pattern from the three named taxa in *P. guianensis*, among other more subtle characters revealed in taxon-by-taxon comparisons (see Diagnosis, above). The general structure and steady pace and frequency of its loudsong, and its multi-note call (Fig. 1B), also place *Poliioptila clementsi* firmly in the *P. guianensis* group. The multi-note call with harmonics given by members of the *P. guianensis* complex is unique in the genus (BMW pers. obs.). Thus, *Poliioptila clementsi* is clearly an integral member of the widespread *P. guianensis* complex (which would be called the *P. schistaceigula* complex if that species is considered an allospecies; see below). Considering the fact that another well-studied pair of sister taxa in the genus, *P. melanura* (Black-tailed Gnatcatcher) and *P. californica* (California Gnatcatcher; Atwood 1988, Atwood and Bontrager 2001), are not as well-differentiated phenotypically in either morphologies or vocalizations as *P. clementsi* and *P. guianensis*, we are satisfied that species status is appropriate for both *P. clementsi* and for other taxa currently recognized as subspecies, as discussed below.

#### REVISION OF THE *POLIOPTILA* *GUIANENSIS* COMPLEX

*Morphology.*—Zimmer (1942) considered *Poliioptila guianensis* closely related to, and possibly conspecific with, trans-Andean *P. schistaceigula*, and it is primarily for this reason that we have included mention of the latter species in this paper. Neither Zimmer (1942) nor Mayr and Paynter (1964, following Zimmer) provided any justification for this opinion; the relationship was deemed “uncertain” by the American Ornithologists’ Union (1998:494). We do not consider *P. schistaceigula* an allospecies in the *P. guianensis* complex, although we suspect that it is sister to the group. If it is a close relative, it is clear that *P. schistaceigula* has differentiated strongly, both morphologically and vocally, from the much more widely distributed cis-Andean radiation comprising the three named

taxa in *P. guianensis*, and now *P. clementsi*. Differentiation appears to be much less advanced east of the Andes, where several allopatric forms share closely similar morphology (Table 1) and a loudsong template of a rapid series of nearly evenly spaced notes lasting about 1.5–2 sec. The paucity of specimens (especially females) and recordings hamper study of the complex. Furthermore, these small, lightly built birds are difficult to prepare as museum skins; on a few specimens it is not possible to be sure that certain features, particularly the presence and extent of white feathering around the eyes and lores, can be seen sufficiently well to allow meaningful comparisons. However, it seems reasonable at this point to offer a better estimation of taxonomic limits than has been attempted to date. Stotz et al. (1997) provided an accurate overview of some of the characters discussed below. Figure 2 maps the distribution of the *Poliioptila guianensis* complex (nominate *guianensis*, *P. g. facilis*, and *P. g. paraensis*), *P. clementsi*, and *P. schistaceigula* and shows, we believe, virtually all records for all of the taxa (localities within about 50 km are mapped as a single point following Isler 1997).

*Tails.*—The amount of white and black on the rectrices is slightly variable on all individual birds (i.e., rectrix on one side of the bird shows slightly different extent of white than its counterpart on the other side) and among specimens within taxa; nonetheless, it provides the most salient plumage feature for intertaxon comparisons (i.e., this fluctuating asymmetry is not of sufficient magnitude to confound taxon identifications). Nominate *guianensis* invariably has the most white, with the outer two rectrices entirely white and rectrix No. 4 entirely or almost entirely white. None of the 12 specimens examined (both sexes included), which spanned the entire known range of this taxon, has any white on the three inner pairs. Both *P. g. facilis* and *P. g. paraensis* have considerably more black on the outer three rectrices than nominate *guianensis* and are similar to each other. One of the *facilis* males from Jaú shows two small blotches of white at the tip of No. 3 on the left feather only, and tiny grayish fringes are present at the tip of No. 3 in other *facilis* specimens. Topotypical specimens of *paraensis* (*n*

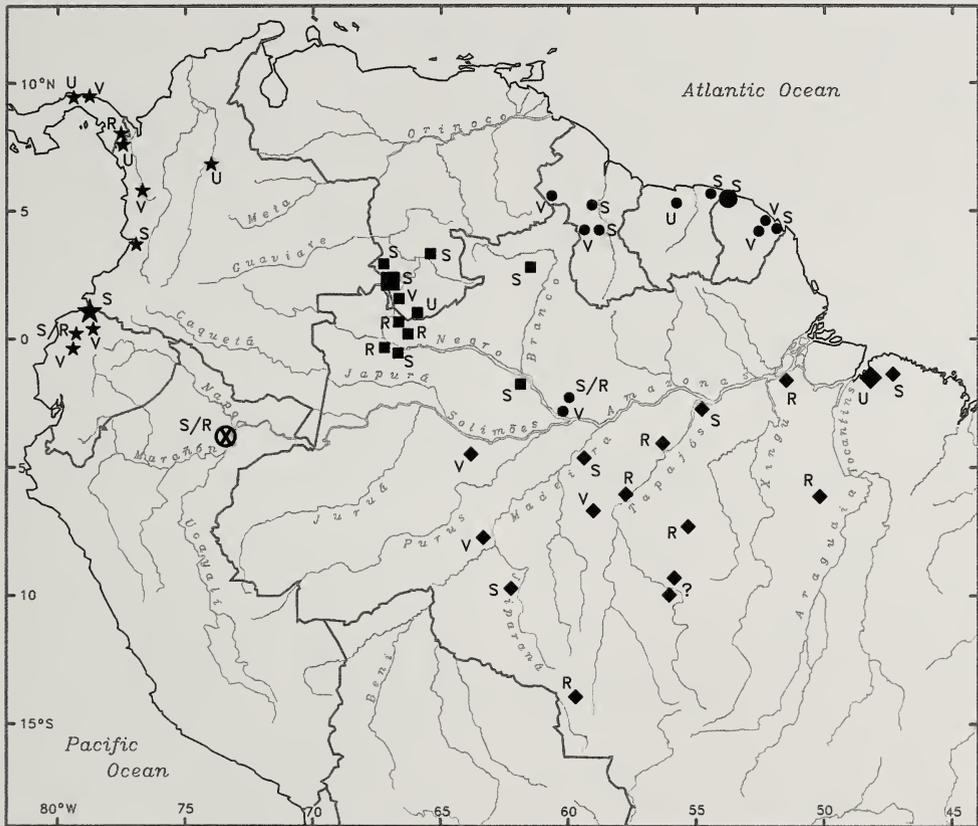


FIG. 2. Distribution of taxa in the *Polioptila guianensis* complex, and that of *P. schistaceigula* (stars). X marks the type locality of *P. clementsi*; dots are *P. g. guianensis*; squares are *P. g. facilis*; diamonds are *P. g. paraensis*. Type localities are enlarged symbols. S beside a symbol means we examined a specimen from that locality; R means we have a recording; U means there is a specimen reported in the literature that we have not examined; and V marks undocumented sight records. The single question mark (?) on the upper Rio Tapajós/Teles Pires marks two or three sight records from opposite sides of the river in the Alta Floresta area, where fieldwork has been extensive but where we still lack confirmation (no specimen, recording, or photo) of occurrence; we hesitate to map these particular records until documentation becomes available. The distance between *P. clementsi* and the nearest known population of *P. guianensis*, on the upper Rio Negro in Brazil, is approximately 800 km.

= 2) have a small white tip (~3 mm) on rectrix No. 4 with no white on the three inner feathers; all other specimens ( $n = 4$ ) show a larger white tip (~6 mm) on No. 4, and a very small (~2 mm) white tip on No. 3. As noted by Zimmer (1942), *P. g. paraensis* tends to have the longest tail of all (Table 1).

*Other plumage features.*—The throat of all *P. g. guianensis* specimens is slightly to markedly more whitish than the breast, although females show less contrast and are more whitish overall (this seems to be true for all taxa). Males show a narrow but fairly conspicuous, often slightly broken, white eye-ring; females

seem to have a more conspicuous eye-ring and narrow white superciliary, as well. Of the five males from French Guiana, one (CM 61912) has an obvious white supra-oral streak extending to the nares, three show some indication of it (as does the single male from Guyana), and one (CM 61923) has none at all. Among all males of other taxa, none shows any sign of the supra-oral streak. The gray of the plumage of *P. g. facilis* is of about the same tone as that of nominate *guianensis* (Zimmer 1942 considered it a little paler), but the throat of males is nearly concolor with the breast rather than distinctly more whitish, and

*facilis* has no, or only a hint, of white around the eye. Plumage of *facilis* specimens from the entire range of points mapped in Fig. 2, encompassing both banks of the upper Rio Negro, shows no appreciable variation, but a larger sample is desirable. *Polioptila g. paraensis* is the palest form overall. Like *P. g. facilis*, and unlike nominate *guianensis*, it shows little or no throat-breast contrast. A male and a female from near the type locality show almost no eye-ring; all others show a weak and broken white eye-ring intermediate in contrast relative to those of *P. g. guianensis* and *P. g. facilis*.

*Soft-part colors*.—Iris color was recorded for eight specimens of *P. guianensis*. All but two of them were recorded as brown or grayish-brown. The adult (skull 100% ossified) female from Rondônia had a “pale gray” iris. Two of the specimens of *P. g. facilis* are noteworthy. FMNH 344215 (male with 90% ossified skull) from Roraima, a short distance west of the Rio Branco, had a “pale yellow orange” iris (label data; Stotz et al. 1997 cited it as “bright orange-yellow”); this was the only brightly colored iris of any specimen in the complex. MPEG 50678 (male with 100% ossified skull) from west of the middle Rio Negro in Jaú National Park had a “brown” iris. Determination of whether these quite different eye colors from localities on opposite banks of the Rio Negro have any geographic restriction awaits further collection of specimens and perhaps careful observations in the field. No differences in the coloration of bills, legs, or feet were noted among taxa, but data from collectors/preparators are generally lacking.

*Vocalizations*.—Figure 3 shows loudsong spectrograms of the members of the *Polioptila guianensis* complex. Measurements of the characters described for vocalizations of *Polioptila clementsii* (above) are summarized by taxon in Table 2. We have illustrated examples from fairly near type localities (mapped in Fig. 2) for *P. g. facilis* and *P. g. paraensis*, but unfortunately we have no recordings of *P. g. guianensis* from near the type locality in French Guiana. However, our examples from near Manaus, Amazonas, Brazil come from the same localities as specimens that are phenotypically almost identical

to the several paratypes of nominate *guianensis*.

The loudsong of *Polioptila g. guianensis* (Fig. 3A;  $n = 2$ ) appears to be a simple, evenly paced repetition of a thin, sharp “inverted chevron” note with greater intensity on the left side of the note. It is also quite level in frequency, with a  $\Delta PF$  of 0.47 kHz. The loudsong of *P. g. facilis* from the left (north) bank of the upper Rio Negro (Fig. 3B;  $n = 4$ ) has the highest introductory note of any of the taxa ( $\sim 9$  kHz); a slightly lower second note is often coupled with it, followed by the rest of the series at a steady, slower pace slightly above 8 kHz. Notes in the series are “inverted U” traces. The song of one individual was more evenly paced throughout (no coupling of the first two notes) with the series at about 7 kHz;  $\Delta PF$  north of the Rio Negro was 0.94 kHz including this individual. Directly across the upper Negro, the first note of the song peaks at about 7 kHz and  $\Delta PF$  is 0.64 kHz ( $n = 2$ ); pace and note shape appear to be essentially the same as they are in songs of birds from the north bank of the river. The “inverted U” notes of *facilis* have highest amplitude at the peak, with nearly equal intensity on the arms; this, together with the rounded shape of the peak of notes in the series, gives the song a slightly softer quality than those of other taxa.

Measures for the loudsong of *P. g. paraensis* (Table 2) were restricted to the sample from the Caxiuanã National Forest west of Belém because this is fairly near the type locality and we had several recordings from there. It is a simple, steadily paced repetition of a sharp, “inverted chevron” note having greatest intensity on the right side (Fig. 3C). Peak frequency range is nearly flat, with  $\Delta PF$  of only 0.37 kHz.

*Discussion*.—All three named taxa in *Polioptila guianensis* differ diagnostically from *P. clementsii* and from each other in both plumage and voice. Published subspecies divisions based entirely on morphological traits accord well with differences in vocalizations, and levels of phenotypic differentiation in the complex seem approximately equivalent. In spite of small sample sizes for most members of the group, we are confident that individual specimens and tape recordings of loudsongs can be assigned unequivocally to taxon as cur-

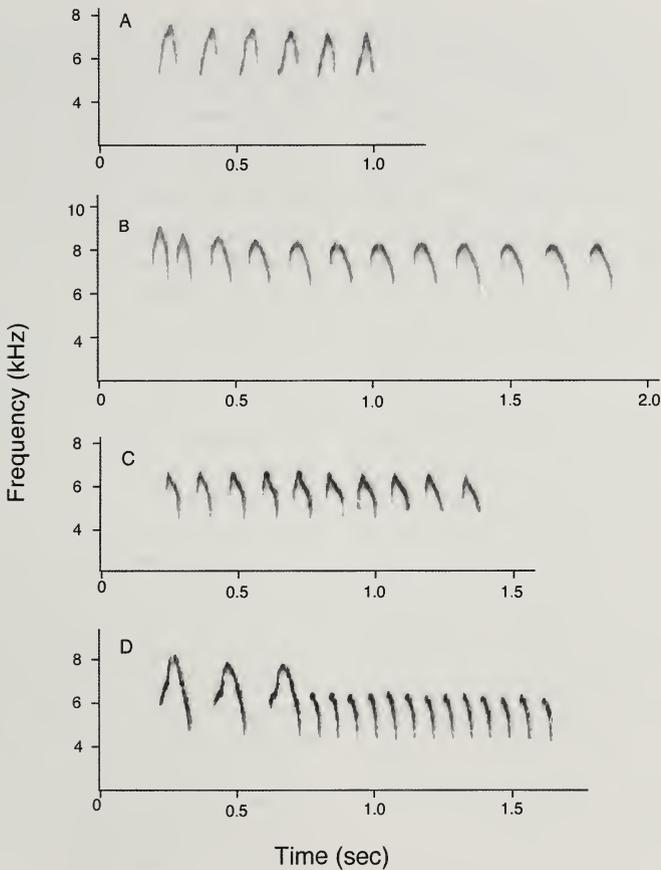


FIG. 3. Sound spectrograms of loudsongs of members of the *Polioptila guianensis* complex. The frequency scale is uniform for all spectrograms, but the area below 4.0 kHz is omitted. (A) *P. g. guianensis* from near Manaus, Amazonas, Brazil; intensity is greatest on the left side of the “inverted chevron” notes; recorded by L. Naka; (B) *P. g. facilis* from 17 km north São Gabriel da Cachoeira, left (north) bank of the upper Rio Negro, Amazonas, Brazil, ~300 km south of the type locality; the “inverted U” notes of *facilis* are distinctive; recorded by K. J. Zimmer; (C) *P. g. paraensis* from the Caxiuanã National Forest, ~400 km west of the type locality; recorded by BMW (D) *P. clementsi* from the type locality (same spectrogram as Fig. 1A); recorded by JAA.

rently defined. Vocalizations may represent a more reliable character set than morphology for distinguishing some forms. Atwood and Bontrager (2001) reached the same conclusion with regard to identification of *Polioptila melanura* and *P. californica*, two narrowly syntopic sister-species (Zink and Blackwell 1998). As an oscine passerine assemblage, however, the question of whether vocalizations can be expected to reflect evolutionary divergence, as they have proven to do quite accurately in the cases of some subsociine passerine groups (Arctander and Fjeldså 1994, Cohn-Haft 2000), should be addressed.

It has been shown for several species of oscine passerines that some elements of songs

are learned during some “critical period” (apparently often the nestling stage), which, subject to a variety of circumstances, can lead to geographically restricted dialects. In a study of the Rufous-collared Sparrow (*Zonotrichia capensis*) in northern Argentina, Loughheed et al. (1993) reported that mtDNA variation observed along a 50-km transect crossing three well-documented song dialects was overlain by, but unrelated to, these dialects. They went on to suggest that “cultural evolution resulting in dialects does not affect dispersal or mating patterns, and, thus, does not promote genetic differentiation.” Looking at a greatly expanded area of coverage, however, they concluded that “hyperdiverse mtDNA and al-

lozyme characters together provide preliminary evidence of large-scale patterns corresponding to subspecies divisions. . . .” Thus, macrogeographic sampling of vocalizations of a widespread oscine passerine seems an appropriate starting point for evaluating the taxonomic ranking of named taxa (i.e., morphologically distinct forms) as well as identifying unnamed populations.

The meager sample of recordings of *P. g. guianensis* was limited to the Manaus area, so it was not possible to investigate whether any geographic structure in vocalizations might be present within its range. Our recordings of *P. g. facilis*, from opposite banks of the upper Rio Negro, show quite similar pace and note shapes, but somewhat different  $\Delta$ PF owing primarily to the higher, sharper introductory note given by birds on the left (north) bank. The upper Negro may separate different dialects or, more likely, we believe it represents a maintenance barrier for genetic divergence as it does for some *Hemitriccus* flycatchers (Cohn-Haft 2000) and other groups of birds. The only taxon for which we have samples from a wide area is *P. g. paraensis*, which shows little variation in the region between the Tapajós and Tocantins rivers.

It is important to note that loudsongs of members of the *P. guianensis* complex from localities for which we have several recordings (*P. clemensi* near Iquitos; *P. g. paraensis* at Caxiuana) show remarkable consistency in all characters measured, as well as important qualitative attributes, such as note shape and tonality. In fact, ranges of measures (Table 2) are quite similar to those reported for larger samples of some thamnophilid antbirds (Whitney and Alvarez 1998; Isler et al. 1999, 2002). We expect that other taxa in the complex will prove to show similar, low levels of variability in their vocalizations. In sum, the evidence points to a lack of any learning element in the development of songs and calls in the *P. guianensis* complex. Similarly, Atwood and Bontrager (2001) concluded that learning is likely not a factor in vocal development in *P. californica*.

The potential to learn some elements of song does not exclude the possibility, or even probability, that vocal templates of oscines are a phenotypic expression of genetic determination and are thus potentially informative in

taxonomic and systematic study. Capacity for song learning and the actual extent of learning of vocalizations have not been studied for any forest-based Neotropical oscine passerine. Extensive field work in most areas of the Amazon basin and other primarily forested habitats in South America indicates to us that, like members of the *Polioptila guianensis* complex, some oscine passerines as unrelated as *Microcerculus* wrens and *Hylophilus* greenlets have maintained a high degree of uniformity of vocalizations across broad geographic fronts, yet show marked geographic differentiation, in accordance with patterns observed for numerous suboscine species (BMW pers. obs.). Another widespread complex in the genus *Polioptila* that shows significant geographically structured variation in morphology, vocalizations, and habitat specificity is the *P. plumbea* group (BMW pers. obs.), but it has not yet been studied.

*Taxonomic conclusions.*—Until we have sufficient data to offer a different, or more complete, picture of speciation in the *Polioptila guianensis* complex, and in consideration of the similar or lesser levels of phenotypic differentiation documented for some other sister-species complexes in the genus, we propose that *Polioptila clemensi* and the three subspecies of *Polioptila guianensis* henceforth be recognized at the species level (this complex probably sister to *P. schistaceigula*) with the following names:

*Polioptila guianensis*, Guianan Gnatcatcher  
*Polioptila facilis*, Rio Negro Gnatcatcher  
*Polioptila paraensis*, Para Gnatcatcher  
*Polioptila clemensi*, Iquitos Gnatcatcher

Both *P. guianensis* and *P. facilis* are known from the left (east) side of the Rio Negro, and the latter has been collected (one specimen) in Roraima a short distance west of the Rio Branco. We suspect that the Rio Branco separates these two forms; this region, however, remains among the most undersampled areas of Amazonia. Similarly, the vast region between the Manaus area and the three Guianas (Fig. 2) has seen almost no collecting; we expect that all forested areas in that hiatus are occupied by *P. guianensis*. In this study, all specimens from south of the Amazon River are provisionally called *P. g. paraensis*. Although linked by pale coloration and long

tails, they are few ( $n = 6$ ) and widely scattered (Fig. 2). For example, we have little information from west of the Rio Tapajós and only two sight records from anywhere west of the Rio Madeira (one of these reported by Peres and Whittaker 1991). We predict, however, that an undetected population inhabits most of the region west of the Madeira north of about 7° S, west to Peru; it should be sought especially in forests growing on white sand and extensively weathered clays (both patchily distributed *terra firme* habitats). There are many additional gaps on the map, and clearly much more work will be required to gain an accurate understanding of how members of the *P. guianensis* complex are distributed. Collection of additional specimens and tape recordings from poorly known areas of the distribution of the *Polioptila guianensis* complex may soon confirm the existence of one or more additional, unnamed populations of these obscure, Neotropical forest gnatcatchers.

As a final thought, in the only study to date that addresses the way in which molecular evolution informs species relationships within the genus *Polioptila*, Zink and Blackwell (1998) reported an mtDNA sequence divergence of about 4% between the sister-species *P. melanura* and *P. californica*. We expect that the level of sequence divergence among members of the *P. guianensis* complex could vary considerably from this owing to a variety of factors such as much larger population sizes of most taxa, evolution in far more stable environments and, probably, lower reproductive rates and increased longevity. Thus, a level of divergence deemed appropriate for recognition of taxa at the species level in one region of the world may not necessarily find its equivalent for obviously related taxa that have evolved in radically different environments. Molecular analysis of the widespread *Polioptila guianensis* group may have the potential to illuminate speciation patterns applicable to a variety of forest-based Amazonian birds.

#### CONSERVATION

The discovery of *Herpsilochmus gentryi* and other species (not only birds, but other vertebrates and plants) new to science or new to Peru, led the Instituto de Investigaciones de la Amazonía Peruana (IIAP) to propose to the

Instituto Nacional de Recursos Naturales (INRENA) the creation of a reserve to protect the rare white-sand habitats near Iquitos. On 16 January 2004, the status of Zona Reservada Allpahuayo-Mishana (established 4 March 1999) was elevated to the Reserva Nacional Allpahuayo-Mishana, encompassing 58,070 ha and protecting the greatest known concentration of white-sand habitats in the Peruvian Amazon. The entire known range of *Polioptila clementsii* is officially protected. However, its presence is confirmed from only about six localities in an area of no more than 2,000 ha because appropriate *varillal* forest is highly patchy in distribution. We estimate that a maximum of 50 pairs survive in the reserve.

Over the past 3 decades, a high percentage of the once-extensive *varillal* habitats in and surrounding the known distribution of *Polioptila clementsii* has been fragmented or destroyed as the Peruvian government encouraged colonization of the area near Iquitos. Agricultural initiatives have largely failed on these nutrient-deficient, quartzitic soils, yet persistent colonists have cleared the land, selling the long, straight trunks of *varillal* trees for construction, firewood, and making charcoal, which, within a national reserve, is prohibited by Peruvian law (Fig. 4). Today, the only known population of *Polioptila clementsii* is fragmented into three parcels separated primarily by deforested terrain. Titled landholders who live within the reserve area take a daily toll on the habitat; destruction is especially accelerated near the paved highway linking Iquitos with the town of Nauta. In mid-2004, the municipality of San Juan (on the west edge of Iquitos) rapidly opened a clandestine road, ostensibly to "promote tourism," along the northern edge of the reserve in an area occupied by several pairs of *P. clementsii*; this is sure to result in significantly increased habitat destruction in this heretofore pristine area. Fragile and highly vulnerable climax *varillal* forests may never properly regenerate from fragmentation because they grow on such nutrient-poor soils. In fact, the place in the reserve in which the specific habitat of *Polioptila clementsii* receives the best protection is the property of the Instituto de Investigación e Extensión Agraria near Km 25 (El Dorado), where the species was discov-



FIG. 4. Destruction of the extensive *varilla* forest, prime habitat of *Polioptila clementsi*, at Nueva Esperanza in the Reserva Nacional Allpahuayo-Mishana near Iquitos, Loreto, Peru. The long, straight trunks of the dominant trees in this habitat, such as *Caraipa tereticaulis*, are easily cut for construction, firewood, and making charcoal. These ancient and slow-growing forests occur on especially nutrient-poor, quartzitic soils, and may never be able to regenerate. Photo by JAA, September 1998.

ered. Illegal extraction of timber continues even there.

Considering its very small, habitat-specialized world population, the great reduction of appropriate habitat in the recent past, and the continuing destruction of existing habitat, we recommend that *Polioptila clementsi* be classified as Critically Endangered. We are optimistic about its preservation within the Reserva Nacional Allpahuayo-Mishana, as much-needed funding is now being channeled directly to the preservation effort administered by IIAP in Iquitos. J. D. Alvan, an enthusiastic and highly skilled young ornithologist, has been hired to carry out field research on *Polioptila clementsi* and to initiate local environmental education programs in the Iquitos area. Park guards will receive dependable salaries; boats and motors will be provided to, and maintained for, cooperative communities along the Rio Nanay; fuel will be purchased; and goods will be distributed.

These simple but critically important aspects of the reserve's preservation have been made possible by the generous monetary contribution of James F. Clements. The challenge will be to maintain funding levels far into the future. Threats to the habitat are increasing just as every year brings more exciting discoveries of plants, insects, amphibians, and other organisms new to science from the white-sand forests of Allpahuayo-Mishana and the Rio Nanay.

The attractive Spanish name "Perlita de Iquitos" (Little Pearl of Iquitos) has inspired Mayor Juan Carlos Del Aguila Cardenas and the Provincial Municipality of Maynas council to adopt the gnatcatcher as the official bird of the city. La Perlita de Iquitos will be used in educational and promotional programs as a symbol of the city's commitment to the bird's conservation and protection of its fragile habitat and the surrounding region.

## ACKNOWLEDGMENTS

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## MOVEMENTS AND HOME RANGES OF MOUNTAIN PLOVERS RAISING BROODS IN THREE COLORADO LANDSCAPES

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**ABSTRACT.**—We report movements and home-range sizes of adult Mountain Plovers (*Charadrius montanus*) with broods on rangeland, agricultural fields, and prairie dog habitats in eastern Colorado. Estimates of home range size (95% fixed kernel) were similar across the three habitats: rangeland (146.1 ha  $\pm$  101.5), agricultural fields (131.6 ha  $\pm$  74.4), and prairie dog towns (243.3 ha  $\pm$  366.3). Our minimum convex polygon estimates of home-range size were comparable to those on rangeland reported by Knopf and Rupert (1996). In addition, movements—defined as the distance between consecutive locations of adults with broods—were equivalent across habitats. However, our findings on prairie dog habitat suggest that home-range size for brood rearing may be related to whether the prairie dog habitat is in a complex of towns or in an isolated town. Received 14 November 2003, accepted 4 February 2005.

The Mountain Plover (*Charadrius montanus*) breeds primarily in the shortgrass prairies of Colorado, Wyoming, and Montana (Graul and Webster 1976) but breeds as far north as Canada and as far south as Mexico (e.g., Graul and Webster 1976, Day 1994, Knopf 1996, Shackford et al. 1999, Manning and White 2001). Colorado is considered the continental stronghold for Mountain Plovers, with over 60% of the population believed to breed there (Kuenning and Kingery 1998). The habitat types used by breeding Mountain Plovers within shortgrass prairie may contain areas grazed by native herbivores, such as bison (*Bison bison*) and black-tailed prairie dogs (*Cynomys ludovicianus*), or domestic herbivores, including cattle and sheep. Mountain Plovers also nest in agricultural fields (Knopf 1996, Knopf and Rupert 1999, Shackford et al. 1999). Landscape-level habitat use by breeding Mountain Plovers may be influenced by the distribution of these habitat types.

Landscape-level characteristics, such as the size, distribution, shape, and availability of different habitat types, are important to a spe-

cies' population dynamics and regulation (Kareiva 1990, McKelvey et al. 1992, Schmiegelow and Monkkonen 2002, Crozer and Niemi 2003). The distribution of individuals among habitats reflects an ability to discriminate between habitat types and assess habitat quality (Pöysä et al. 2000), and differences in habitat affinity may partially explain the wide range of avian responses to loss of native habitat (Sekercioglu et al. 2002). Landscape configuration and proximity of resources provided by different habitat types may be critical to the breeding success of Mountain Plovers. Suitable breeding habitats minimize the energetic costs of foraging and reduce exposure to predators (Pöysä et al. 2000). Here, we report the relationship between movements and home-range sizes of Mountain Plovers during the brood-rearing period within three different habitat types.

### METHODS

Information on brood-rearing activity of Mountain Plovers was collected in eastern Colorado from 2001 to 2003 during other ongoing studies in three different habitat types: rangeland, black-tailed prairie dog towns, and agricultural fields. In high-elevation (2,600–3,500 m) rangeland in Park County, Colorado, the habitat consisted primarily of slimstem muhly (*Muhlenbergia filiculmis*), and, to a lesser extent, blue grama (*Bouteloua gracilis*) grazed by domestic bison or cattle (Wunder et al. 2003). Our prairie dog study areas, located in Lincoln and Weld counties in eastern Colorado (also characterized as rangeland) were dominated by blue grama and buffalograss

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(*Buchloe dactyloides*). Only 1.94% of eastern Colorado is occupied by prairie dogs (White et al. 2005), and, in our study area, we knew of only one prairie dog complex (>10,000 ha)—a network of small (mean = 80 ha; range = 1–340 ha), active prairie dog towns within 800 m of each other. The agricultural field habitats were primarily composed of winter wheat strips interspersed with fallow fields in Weld County. The agricultural fields were >256 ha and located in areas with high concentrations of other agricultural fields. We were unable to address among-year variation in movements or home-range size because each year we conducted our study on a different habitat type: rangeland in 2001, agricultural fields in 2002, and prairie dog habitat in 2003.

To investigate Mountain Plover movements and home-range size, we attached 2.2-g radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota) to nesting adult plovers at, or just before, hatching of eggs. We used walk-in box traps made of mesh wire to capture adult plovers at their nests. We placed radio transmitters on adults in each of the three habitats: 35 birds in rangeland (2001), 26 in agricultural fields (2002), and 15 in prairie dog habitat (2003). Body mass of adult Mountain Plovers ranges from 90 to 110 g (Knopf 1996); thus, transmitters were  $\leq 2.4\%$  of their body mass. A transmitter was affixed by applying a light coating of waterproof epoxy (Ace, Starbrite, or Devcon) to the transmitter and then sliding it under the upper back feathers. This attachment procedure allowed the transmitters to drop off when the birds later molted those feathers. Battery life of the transmitters was expected to be 56 days.

Using a hand-held Yagi antenna, each day we attempted to locate adults with broods to record the presence of (and count) chicks and record their location and habitat. Due to adverse weather conditions, however, data for some locations were collected at 2-day intervals. First, we located birds from greater distances (up to 800 m) to avoid forcing brood movements caused by human disturbance. After recording observer coordinates and distance and bearing to each adult with a brood, we approached (usually by walking) the birds to confirm their location via visual observation. Adults with broods were located until

their chicks fledged, 36 days post-hatch (Miller and Knopf 1993). Adults with broods that did not successfully fledge at least one chick were not included in our analysis.

To calculate brood home-range sizes, we used the fixed-kernel method (Worton 1995, Seaman and Powell 1996) with a smoothing parameter chosen by least squares cross validation. This nonparametric technique depicts irregular distributions more accurately and produces home-range estimates with less bias relative to other home-range estimators (Seaman and Powell 1996). Home-range values were based on 50 and 95% contour intervals, hereafter referred to as “core area” and “home range,” respectively (Bogner and Bal-dassarre 2002, Vega Rivera et al. 2003). Movement was defined as the distance moved between two consecutive locations. We also calculated minimum convex polygon home ranges, the minimum amount of area used to raise broods, for comparison with an earlier study (Knopf and Rupert 1996). Means are presented  $\pm$  SD.

## RESULTS AND DISCUSSION

*Home range.*—We monitored 12 broods on rangeland in 2001, 13 broods on agricultural fields in 2002, and 10 broods on prairie dog habitat (2 broods on the prairie dog complex, 8 on prairie dog towns) in 2003. Analyses were based on a mean of  $20.3 \pm 3.8$  locations per brood in rangeland (range = 18–28),  $28.7 \pm 5.2$  locations per brood in agricultural fields (range = 23–34), and  $26.3 \pm 6.6$  locations per brood in prairie dog habitat (range = 19–33). Home-range estimates for the three habitats were relatively comparable for rangeland ( $146.1 \text{ ha} \pm 101.5$ ), agricultural fields ( $131.6 \text{ ha} \pm 74.4$ ), and prairie dog towns ( $243.3 \text{ ha} \pm 366.3$ ).

Although mean point estimates of the core area on prairie dog towns were  $>2\times$  those on rangeland and agricultural fields, confidence intervals between the three habitat types overlapped (Table 1). The larger point estimates in home range and core area on prairie dog habitat could be attributed to two birds, both of which raised their broods on the prairie dog complex. One had an estimated home range of 1,156.5 ha and a core area of 210.8 ha, and the other had a home range of 630.0 ha and a core area of 114.4 ha. Removing the data for

TABLE 1. Mean home-range size (ha) and movements of Mountain Plover adults with broods on rangeland ( $n = 12$  broods), agricultural fields ( $n = 13$ ), and prairie dog habitats ( $n = 10$ ) in eastern Colorado from 2001 to 2003. Home-range size was based on 50% and 95% fixed kernel (FK) and minimum convex polygon (MCP) home-range estimates.

Habitat (year)	No. locations		50% FK		95% FK		MCP		Movement (m)	
	Mean	SD	Mean	SD (95% CI)	Mean	SD (95% CI)	Mean	SD (95% CI)	Mean	SD (95% CI)
Rangeland (2001)	20.3 (18–28) <sup>a</sup>	3.8	21.8	12.2 (14.9, 28.6)	146.1	101.5 (18.6, 203.5)	66.5	44.4 (41.4, 91.7)	482.3	165.0 (389.0, 575.7)
Agricultural fields (2002)	28.7 (23–34) <sup>a</sup>	5.2	19.9	14.2 (12.1, 27.6)	131.6	74.4 (19.1, 172.0)	90.3	53.6 (61.1, 119.4)	411.3	131.1 (340.0, 482.5)
Prairie dog habitat (2003)	26.3 (19–33) <sup>a</sup>	6.6	44.8	66.8 (3.5, 86.2)	243.3	366.3 (16.2, 470.3)	115.5	169.2 (10.6, 220.4)	422.9	174.9 (314.4, 531.3)

<sup>a</sup> Range of number of telemetry locations.

these two birds yielded a home range of 80.8 ha  $\pm$  42.8 and core area of 15.4 ha  $\pm$  10.7 on prairie dog towns. The other eight radio-marked birds and their broods were located on smaller, isolated prairie dog towns surrounded by shortgrass prairie that was either ungrazed or lightly grazed by cattle.

Minimum convex polygon (MCP) home ranges on rangeland, agricultural fields, and prairie dog habitat were comparable to those reported by Knopf and Rupert (1996) for rangeland habitat (56.6 ha  $\pm$  21.5, CI = 39.4–73.8). Although there are inherent biases with MCP, such as those generated when exploited areas are large (Kenward 1987), the overlapping confidence intervals in home ranges among habitat types suggest that Mountain Plovers raising broods use comparably sized patches within very different landscapes.

*Movements.*—Movement, defined as the distance between consecutive locations of adults with broods, was similar across habitats. Birds that nested in rangeland habitats of Park County remained on rangeland; they did not move their broods to other habitats. However, the landscape of Park County has changed very little over the past century; ranching is still the primary land-use practice and there are few or no agricultural fields or prairie dog towns to which birds could have moved (Wunder et al. 2003).

Plovers that nested on agricultural fields exhibited no obvious patterns with respect to moving their broods. Some individuals ( $n = 4$ ) stayed on agricultural fields, while others moved to adjacent or nearby rangeland ( $n = 4$ ) or moved back and forth between agricultural fields and rangeland ( $n = 5$ ). It may be that when conditions are dry, invertebrate prey and/or cover are depauperate, resulting in these among-habitat movements. In the year we studied brood-rearing activity on agricultural fields in Weld County (2002), our study area experienced extreme drought conditions (National Drought Mitigation Center 2004). The vegetation on both agricultural fields and rangeland was relatively short and sparse compared with years when weather conditions were normal or wet (VJD pers. obs.).

No plovers that nested in prairie dog habitat moved their broods to other habitat types. The weather conditions for the year of the prairie dog study (2003) were categorized as wet dur-

ing the breeding season (National Drought Mitigation Center 2004), which resulted in taller and denser vegetation on prairie dog habitat (VJD pers. obs.). The increase in vegetation may have provided more concealment for plovers or increased prey resources; thus, perhaps, adults did not need to seek out other habitats in order to successfully fledge their broods.

Movements were similar for all 3 years and habitats (Table 1). Movements of the two adults and broods with the largest home ranges on prairie dog habitat were 690.7 and 589.9 m, within the range of movements observed in all habitats (175.6–800.1 m). Additionally, movements did not appear to be related to size of home range or core area. For example, one adult nested on a small prairie dog town approximately 200 ha in size. Its home range (132.4 ha) and core area (34.9 ha) were relatively small, but its movements were similar (604.2 m) to those of other adults with broods.

Because our study was conducted in three different habitats, each in a different year, and because our sample sizes were small, we cannot validate any inferences between habitats, sites, or years for home-range estimates or movement patterns. Our findings from prairie dog habitat suggest that home range and core area used by Mountain Plovers for brood rearing may be related to the size of prairie dog habitat; movement distances were not related to prairie dog habitat size. In Montana, adult plovers with broods are not known to move between prairie dog towns (Dinsmore et al. 2002); in Colorado, however, we did observe adults with broods move between prairie dog towns within a complex of prairie dog towns. We conclude that prairie dog complexes are likely more favorable for Mountain Plover brood-rearing activity than isolated prairie dog towns. Similarly, Biggins et al. (1993) suggested that the prairie dog complex, and not the prairie dog town, is the habitat unit selected by black-footed ferrets (*Mustela nigripes*).

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## WINTER FORAGING OF LONG-TAILED DUCKS (*CLANGULA HYEMALIS*) EXPLOITING DIFFERENT BENTHIC COMMUNITIES IN THE BALTIC SEA

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**ABSTRACT.**—We studied the feeding ecology of Long-tailed Ducks (*Clangula hyemalis*) in two different marine benthic habitats in the Baltic Sea to determine whether there were differences in diet choice, foraging selectivity, body condition, and bird abundance. Our results corroborate earlier suggestions that Long-tailed Ducks exhibit ecological plasticity in selecting winter habitat and food. The majority of Long-tailed Ducks occurred in hard-bottom habitats where they relied on the bivalve *Mytilus edulis*; however, some of the population wintered in less productive, soft-bottom habitats where they employed a prey-selective foraging strategy, in which they fed on less abundant, but energy rich, crustaceans. Both strategies were apparently viable, as dissected birds in both habitats were in good body condition and had substantial fat reserves. Received 20 April 2004, accepted 11 February 2005.

The Long-tailed Duck (*Clangula hyemalis*) is the most abundant sea duck wintering in the Baltic Sea, where estimated numbers exceed 4 million. Wintering Long-tailed Ducks inhabit a variety of coastal habitats and shallow off-shore banks (Durinck et al. 1994). Diet composition varies widely throughout their Holarctic range (Madsen 1954, Peterson and Ellarson 1977, Vermeer and Levings 1977, Goudie and Ankney 1986, Stempniewicz 1995, Bustnes and Systad 2001, Jamieson et al. 2001). However, few attempts have been made to relate feeding habits of Long-tailed Ducks to attributes of their local environment (Nilsson 1972, Stott and Olson 1973, Kube 1996). Long-tailed Ducks are recognized as opportunistic feeders (Peterson and Ellarson 1977, Goudie and Ankney 1986, Bustnes and Systad 2001), but ecological factors related to use of different habitats have received little study. We investigated food choice of Long-tailed Ducks wintering in two distinct marine habitats in nearshore waters of the Baltic Sea off the coast of Lithuania. Our objectives were to determine whether there were differences in diet choice of Long-tailed Ducks in the two winter habitats, and whether body condition of the ducks varied between the habitat types.

### METHODS

**Study area.**—The Lithuanian coast can be characterized as an exposed, sandy coast, typical of the southern and eastern Baltic Sea (Oleninas et al. 1996). The sea floor is dominated by sand, gravel, or boulders. Sandy-bottom substrates predominated in the southern half of our study area along the Curonian Spit coast. The northern half of the Lithuanian nearshore zone is characterized by a mosaic of sediments of sand, gravel, and boulders (Oleninas et al. 1996). The sublittoral slope is gentle, with the 10-m isobath extending 700–2,000 m and the 20-m isobath extending 1,500–4,000 m from the shore. Water salinity along the Lithuanian coast is low, ranging from 6 to 8‰, which results in relatively poor faunal and floral diversity, as well as in low productivity.

Two main types of macrofaunal communities can be distinguished in the Lithuanian coastal zone: the *Mytilus edulis* community of sessile, epifaunal filter-feeders, and the *Macoma baltica* community of mobile, infaunal surface-deposit feeders (Olenin 1996, Oleninas et al. 1996). The *M. edulis* community dominates in the northern half of the Lithuanian coastal zone, occurring on hard bottoms covered by stones and boulders at depths between 5 and 30 m. This community has the highest biodiversity (up to 50 macrozoobenthos species) and biomass (mean = ~1,750 g/m<sup>2</sup>, maximum = ~2,500 g/m<sup>2</sup> wet weight). *M. edulis* makes up ~93% of the total biomass; *Balanus improvisus* (a barnacle) and all the

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remaining species contribute ~7 and <1% of total wet weight, respectively. In some places, stony substrates at depths from 4 to 14 m are overgrown by the red algae, *Furcellaria lumbricalis*, which serves as an important spawning ground for Baltic herring (*Clupea harengus membras*; Olenin 1996, Oleninas et al. 1996).

The *M. baltica* community is associated with soft bottoms, and extends along the coast of the Curonian Spit at depths from 5 to 30 m. This habitat can be characterized as a homogenous, benthic biotope with up to 40 macrozoobenthos species dwelling in a sandy bottom. *M. baltica* and *Mya arenaria* are the dominant infaunal bivalves, composing 61 and 12% of the total biomass, respectively. Polychaetes (*Nereis diversicolor*, *Pygospio elegans*) and crustaceans (*Saduria entomon* and *Corophium* spp.) also are abundant. Mean zoobenthos biomass is ~150 g/m<sup>2</sup> wet weight, with a maximum of ~300 g/m<sup>2</sup> (Olenin 1996, Oleninas et al. 1996).

Based on spatial distribution and dominance of benthic communities (Olenin 1996; S. Olenin unpubl. data), three zones have been distinguished along the Lithuanian coast: a hard-bottom benthic community zone, an intermediate zone, and a soft-bottom community zone (Fig. 1). We present data on Long-tailed Duck foraging in hard-bottom and soft-bottom benthic community zones, but not the intermediate zone.

*Data collection and analysis.*—Birds accidentally drowned in fishing nets were collected for diet analysis during winters of 1997/1998 through 2000/2001. Nets were set at depths ranging from 1.5 to 20 m. In total, 326 Long-tailed Ducks were collected: 181 from habitats with hard-bottom and 145 from areas with soft-bottom substrates. Sex-age cohorts of collected birds in hard- and soft-bottom habitats, respectively, were as follows: immature males 13 and 14%; adult males 55 and 58%; immature females 16 and 8%; and adult females 16 and 20%.

The majority of collected birds were frozen within hours of collection. Frozen birds were thawed in a laboratory, dissected, aged, and sexed using the methods of Jones et al. (1982). Body fat was assessed by examining the subcutaneous fat layer on the upper abdomen, lower abdomen, and lower intestines.

Ranked categories of fat indices ranging from 0 to 3 were used for each deposit (0 = no fat and 3 = abundant fat), with overall fat scores calculated as the sum of the three indices (Jones et al. 1982). If not examined immediately, gizzards and esophagi were removed and deep-frozen or preserved in 4% formaldehyde solution until contents could be analyzed. Contents of gizzards and esophagi were treated separately, with material sorted, identified to the lowest possible taxonomic level, measured, and weighed. Each prey species was weighed separately except for small crustaceans, where gammarids were pooled without identifying specimens to species. Barnacles and bryozoans (*Electra crustulenta*) attached to mollusk shells were not considered as separate prey items; only loose barnacles were included in the analyses. The digestion stage of gizzard contents was assessed according to the following scheme: (1) food items intact, visually unaffected by digestion; (2) food at initial stage of digestion, soft prey still easy identifiable, much identifiable tissue; (3) food items heavily affected by digestion with some remains of tissues; and (4) food items heavily affected by digestion, no identifiable tissues remaining.

Diet composition was assessed according to wet weight of prey, including mollusk shells, from esophagi and gizzards showing stages 1 and 2 of digestion. Prey items were weighed to 0.01 g after removing surplus water by placing food items on filter paper. Data were summarized as the mean percentage of wet weight of each prey taxa per individual (Krapu and Reinecke 1992). Frequency of occurrence was calculated as the percentage of birds containing a certain food item. Inorganic materials (sand, pebbles, and amber) were excluded from subsequent analyses of content.

Preference of food objects in the two habitats was measured by Ivlev's selectivity index (Manly et al. 1993), calculated using the formula:

$$E = \frac{r_i - p_i}{r_i + p_i},$$

where  $r_i$  is the proportion of an item in the diet,  $p_i$  is the proportion of an item in the environment, and  $E$  is the selectivity index. Positive values indicate that the item is sought out

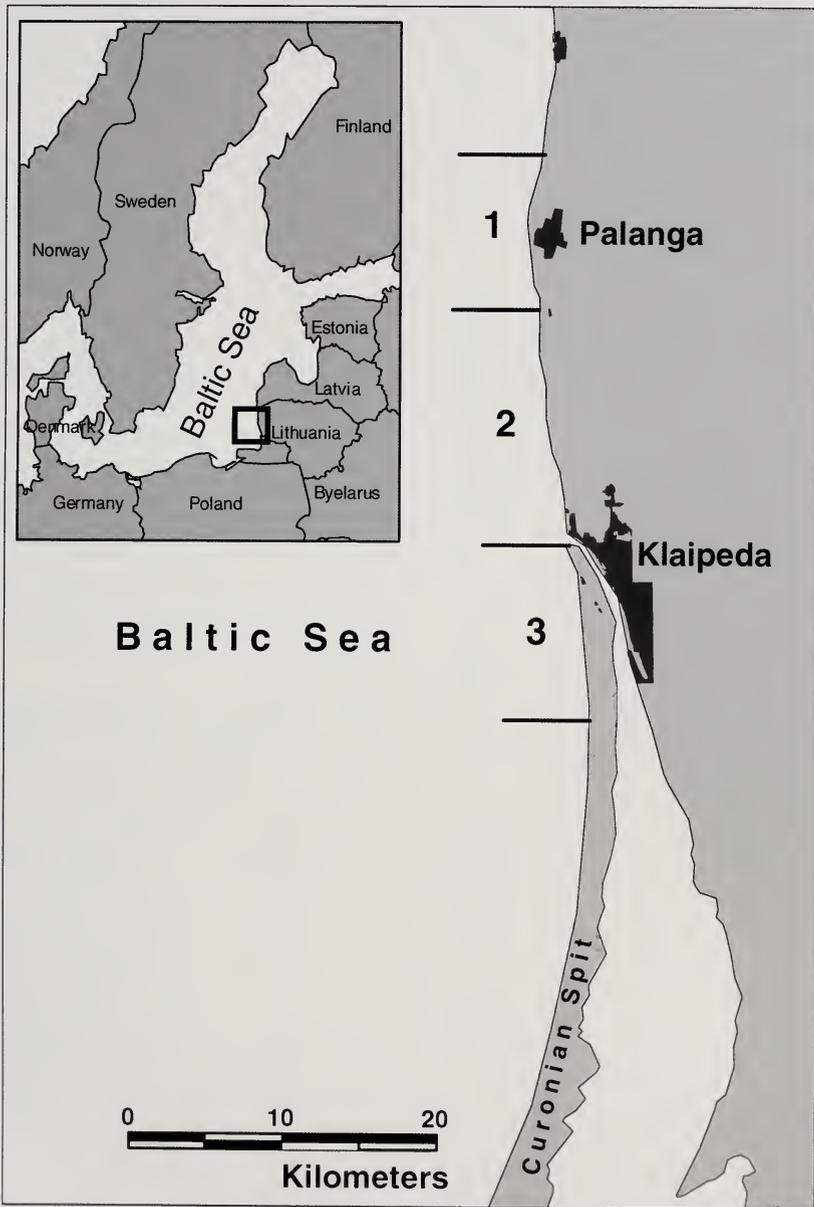


FIG. 1. Study area along the Lithuanian coast of the Baltic Sea and the three different habitat zones where the feeding ecology of Long-tailed Ducks was studied: (1) hard-bottom habitat, (2) intermediate zone, and (3) soft-bottom habitat.

in the environment and negative values indicate that it is not. To determine  $p_i$ , we used available benthos composition and biomass data that were collected in multiple sampling stations along the Lithuanian coast during 1980–1992. These data were summarized as average values (Olenin 1996, Oleninas et al. 1996), and correspond closely to those of oth-

er studies along the Lithuanian coast (Maksimovas et al. 1996, Bubinas and Vaitonis 2003). Because bivalve communities are considered to be relatively stable in the Baltic Sea (Kautsky 1982), we assumed that food resources utilized by Long-tailed Ducks during our study were well represented by previous studies (Olenin 1996, Oleninas et al. 1996).

We also assumed that the *M. edulis* community offers a rich and predictable food resource for Long-tailed Ducks, since the majority of *M. edulis* are of edible size, accessible to diving birds, and abundant (Daunys 1995). The *M. baltica* community was considered a poorer food resource due to low average biomass and because potential food objects are mostly buried in sand.

We conducted surveys to assess the abundance and distribution of wintering Long-tailed Ducks during four consecutive wintering seasons from 1997/1998 through 2000/2001. Survey areas were 10-km sections of shoreline along both hard- and soft-bottom community zones, with a 17-km gap between them (Fig. 1). Bird survey areas corresponded with the locations where ducks were obtained for diet analysis. We conducted bird counts from shore one to two times per month from December until April. Adverse conditions, such as choppy seas and ice floes, occasionally prevented us from conducting surveys. We used a spotting telescope (20–45×) and binoculars (10 × 50) to survey for birds on the water up to 2 km from shore. Bird abundance in the two habitats was summarized as mean number of ducks observed per linear km of shoreline surveyed. Statistical analyses were performed using Statistica 6.0 (StatSoft, Inc. 2001). We used nonparametric statistics to compare count and categorical data: a Kolmogorov-Smirnov test was applied to compare counts between two samples, Kruskal-Wallis ANOVA was used to compare multiple samples, and Mann-Whitney *U*-tests were used to compare data where sample sizes were low ( $n < 20$ ; StatSoft, Inc. 2004). Standard deviations (SD) are given for means and statistical significance was set at  $P < 0.05$ . Considering the controversy surrounding the use of significance testing in the biological sciences (Cohen 1994, Johnson 1999), we also calculated effect sizes using the equation:

$$d = \frac{M_1 - M_2}{\sigma_{\text{pooled}}}$$

where  $d$  is the difference between means  $M_1$  and  $M_2$  divided by the pooled standard deviation,  $\sigma_{\text{pooled}}$ , which is defined as the square root of the mean of the two variances (Cohen 1988). Operational definitions for effect sizes

are small ( $d = 0.2$ ), intermediate ( $d = 0.5$ ), and large ( $d = 0.8$ ; Cohen 1988).

## RESULTS

**Diet composition.**—A total of 119 Long-tailed Ducks that fed over hard-bottom, and 87 that fed over soft-bottom substrates contained undigested food in gizzards and esophagi. At least 17 and 18 different prey taxa were ingested in hard- and soft-bottom habitats, respectively (Table 1). The actual number of prey species ingested was higher, as gammarids were pooled together without identification to species, and there were some specimens in other taxonomic groups not identified to species level. The few identified gammarids were *Gammarus oceanicus*, *G. salinus*, and *G. zaddachi*. The mean number of prey species ingested per Long-tailed Duck was  $2.2 \pm 1.1$  ( $n = 119$ ) in areas with hard-bottom and  $1.9 \pm 1.2$  ( $n = 87$ ) in soft-bottom habitat (Kolmogorov-Smirnov test:  $Z = 1.33$ ,  $P = 0.058$ ;  $d = 0.28$ ).

Over hard-bottom substrates, *M. edulis* dominated in terms of wet weight and frequency of occurrence in the diet of Long-tailed Ducks (Table 1). The selectivity index for *M. edulis* was close to zero ( $E = -0.05$ ,  $p_{\text{edulis}} = 0.93$ ,  $r_{\text{edulis}} = 0.85$ ), which indicates no active selection or avoidance. *S. entomon* was the dominant food type of birds that fed over soft-bottom substrates (Table 1). The selectivity index for this prey item was  $E = 0.73$  ( $p_{\text{entomon}} = 0.1$ ,  $r_{\text{entomon}} = 0.63$ ), indicating that *S. entomon* was actively sought. Selectivity indices of bivalve clams in soft-bottom habitat were strongly negative for *M. baltica* ( $E = -0.79$ ,  $p_{\text{baltica}} = 0.61$ ,  $r_{\text{baltica}} = 0.07$ ) and *M. arenaria* ( $E = -0.54$ ,  $p_{\text{arenaria}} = 0.12$ ,  $r_{\text{arenaria}} = 0.04$ ).

Although *M. edulis* was the main prey species taken from hard-bottom habitat throughout the winter, Baltic herring spawn became the dominant food item in April, when it composed 68% of dietary wet weight (Fig. 2A). Crustaceans were the dominant food in soft-bottom habitat and did not fluctuate significantly between months (Kruskal-Wallis ANOVA:  $\chi^2 = 3.08$ ,  $df = 4$ ,  $P = 0.54$ ; Fig. 2B; effect size  $d$  range: 0.05–0.50). We detected no significant sex- or age-related differences in diet composition in either habitat.

**Fat score.**—Mean fat scores of Long-tailed

TABLE 1. Diet composition of Long-tailed Ducks in soft- and hard-bottom habitats in the Lithuanian Baltic Sea, 1997–2001, expressed as frequency of occurrence (FO) and mean percent of wet weight (WW). Dominant food items are in boldface.

Prey	Soft-bottom ( <i>n</i> = 87 birds)		Hard-bottom ( <i>n</i> = 119 birds)	
	FO (%)	Mean % of WW (SD)	FO (%)	Mean % of WW (SD)
Algae	4 (4.6)	0.3 (1.7)	15 (12.6)	1.3 (9.4)
<i>Ceramium rubrum</i>			2 (1.7)	0.0 (0.0)
<i>Furcellaria lumbricalis</i>	1 (1.2)	0.1 (0.8)	13 (10.9)	1.1 (9.2)
Unidentified algae	3 (3.5)	0.2 (1.5)	4 (3.4)	0.3 (1.8)
Polychaetes	16 (18.4)	7.7 (24.4)	7 (5.9)	0.1 (0.3)
<i>Nereis diversicolor</i>	13 (14.9)	6.5 (22.2)		
Unidentified polychaete	3 (3.5)	1.2 (10.7)	7 (5.9)	0.1 (0.3)
Bivalves	32 (36.8)	14.5 (30.5)	113 (95.0)	86.8 (30.9)
<i>Cardium edule</i>	3 (3.5)	0.8 (5.7)		
<i>Macoma baltica</i>	14 (16.1)	7.2 (23.0)	5 (4.2)	0.4 (3.0)
<i>Mya arenaria</i>	15 (17.2)	3.6 (14.0)	10 (8.4)	1.0 (8.6)
<i>M. arenaria</i> siphons	1 (1.2)	0.8 (7.4)		
<i>Mytilus edulis</i>	4 (4.6)	2.3 (14.4)	<b>110 (92.4)</b>	<b>84.6 (33.6)</b>
Gastropods			11 (9.3)	0.1 (1.0)
<i>Hydrobia</i> sp.			8 (6.7)	0.0 (0.0)
<i>Theodoxus fluviatilis</i>			2 (1.7)	0.1 (1.0)
Unidentified gastropods			1 (0.8)	0.0 (0.1)
Crustaceans	71 (81.6)	74.3 (39.7)	27 (22.7)	3.7 (14.7)
<i>Balanus improvisus</i>	1 (1.2)	0.0 (0.0)	13 (10.9)	0.6 (2.2)
<i>Crangon crangon</i>	5 (5.8)	2.3 (14.2)	1 (0.8)	0.7 (8.0)
<i>Gammarus</i> spp.	4 (4.6)	0.0 (0.0)	11 (9.2)	0.6 (3.0)
<i>Idothea</i> sp.			1 (0.8)	0.0 (0.0)
<i>Mysis mixta</i>			1 (0.8)	0.0 (0.0)
<i>Neomysis integer</i>	10 (11.5)	9.1 (28.7)	2 (1.7)	1.3 (10.2)
<i>Saduria entomon</i>	<b>62 (71.3)</b>	<b>63.1 (44.9)</b>	2 (1.7)	1.4 (11.1)
Unidentified crustaceans	1 (1.2)	0.1 (0.6)	2 (1.7)	0.0 (0.1)
Fish	7 (8.1)	3.3 (12.9)	2 (1.7)	0.8 (6.7)
<i>Ammodytes</i> sp.	4 (4.6)	1.8 (9.6)		
<i>Clupea harengus</i> eggs			10 (8.4)	7.2 (24.7)
<i>Gasterosteus aculeatus</i>	1 (1.2)	0.1 (1.0)		
<i>Osmerus eperlanus</i>	1 (1.2)	0.5 (4.3)		
<i>Platichthys flesus</i>	2 (2.3)	0.1 (0.7)		
<i>Pomatoschistus</i> sp.			1 (0.8)	0.2 (2.7)
<i>Sprattus sprattus</i>	1 (1.2)	0.2 (1.8)		
Unidentified fish	2 (2.3)	0.7 (4.7)	1 (0.8)	0.6 (6.2)

Ducks collected from areas with hard- and soft-bottom sediments were  $6.9 \pm 1.9$  ( $n = 124$ ) and  $7.4 \pm 1.4$  ( $n = 93$ ) respectively ( $U$ -test = 5,061.0,  $Z = -1.54$ ,  $P = 0.12$ ;  $d = 0.33$ ; Table 2). Over hard-bottom habitat, the mean fat score of adult males was significantly lower than that of immature males ( $U = 317.5$ ,  $Z = 2.86$ ,  $P = 0.004$ ) and immature females ( $U = 362$ ,  $Z = -3.17$ ,  $P = 0.002$ ). Over soft-bottom habitat, adult males also had the lowest fat reserves, which differed significantly from that of immature females ( $U = 81.5$ ,  $Z = -2.79$ ,  $P = 0.005$ ); there were no

significant differences observed among other sex-age groups. Effect sizes among sex and age cohorts (Table 3) indicated somewhat similar relationships to those obtained by Mann-Whitney  $U$ -tests. No trend was observed in fat-score values over the course of the wintering season, and overall high fat-score values ( $>5$ ) indicated that birds were in good body condition with considerable fat reserves.

*Abundance and distribution.*—Abundance of Long-tailed Ducks per linear km of shoreline over hard-bottom habitat ( $331 \pm 544$ ,  $n = 26$  surveys), was nearly 10 times higher

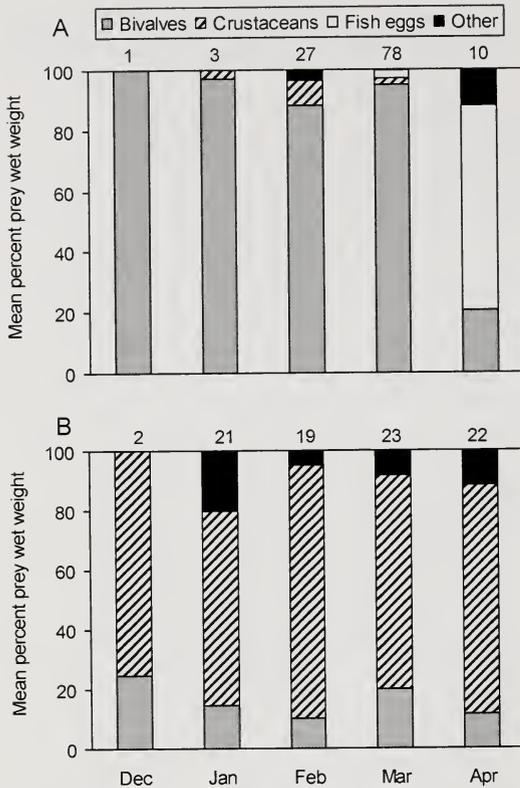


FIG. 2. Percent wet weight of prey taken by Long-tailed Ducks in the Lithuanian Baltic Sea, December–April, 1997–2001. Bivalves dominated the diet in hard-bottom habitat (A), with herring eggs being important in April. Crustaceans dominated the diet of birds in soft-bottom habitat (B). Sample sizes appear above bars.

than that over soft-bottom habitat ( $36 \pm 23$ ,  $n = 17$  surveys;  $U = 60.5$ ,  $Z = 3.99$ ,  $P < 0.001$ ;  $d = 0.77$ ).

## DISCUSSION

Our results provide insight into the feeding ecology of Long-tailed Ducks in two contrasting coastal habitats of the eastern Baltic Sea. Marked differences were observed in Long-tailed Duck foraging patterns in different habitats. Differences involved numbers of birds using those areas, diet composition, and the degree of selectivity when choosing food items. However, body condition of birds was similar between habitats. The majority of Long-tailed Ducks occurred over rich, hard-bottom communities, where densities were approximately 10 times higher than in soft-bottom areas.

TABLE 2. Fat scores of Long-tailed Ducks in hard- and soft-bottom habitats along the Baltic Sea coast of Lithuania, 1997–2001. Birds were in generally good body condition (i.e., fat scores  $\geq 5$ ).

Habitat type/age class	Mean	SD	Range	<i>n</i>
<b>Hard-bottom</b>				
Immature males	7.7	2.0	3–9	17
Adult males	6.3	1.9	2–9	68
Immature females	7.8	1.7	4–9	20
Adult females	7.1	1.6	4–9	19
All birds	6.9	1.9	2–9	124
<b>Soft-bottom</b>				
Immature males	7.6	1.4	4–9	14
Adult males	7.1	1.4	4–9	53
Immature females	8.5	0.8	7–9	8
Adult females	7.8	1.3	5–9	18
All birds	7.4	1.4	4–9	93

Prey-item selectivity was very low in hard-bottom habitat, where birds fed primarily on the most available prey item, *M. edulis*. In April, ducks switched to feeding on fish eggs, when this temporary, but energy-rich, food source became available. Rich beds of *M. edulis* and spring herring spawn offer predictable food resources, so birds can ensure necessary energy intake with a given investment of effort. In contrast to hard-bottom habitat, Long-tailed Ducks exhibited a high degree of selectivity in soft-bottom habitat, where they foraged on the isopod, *S. entomon*, despite a benthic community dominated—in both biomass and abundance—by infaunal bivalves (Olenin 1996, Bubinas and Vaitonis 2003). In soft-bottom habitat, dominant bivalves were present at much lower densities, and some of them were unavailable because they burrow deeply into the sediment (Olenin 1996, Kube

TABLE 3. Effect sizes contrasting fat indices among age and sex cohorts of Long-tailed Ducks collected along the Baltic Sea coast of Lithuania, 1997–2001. Contrasts for hard-bottom sites are in the lower left portion of the table, with soft-bottom contrasts in upper right. See methods for interpretation of values.

	Immature males	Adult males	Immature females	Adult females
Immature males	—	0.41	0.76	0.10
Adult males	0.70	—	1.29	0.53
Immature females	0.05	0.82	—	0.69
Adult females	0.33	0.44	0.43	—

1996). Therefore, birds in soft-bottom habitat may not be able to rely on mollusks, and instead search for mobile, but more energy-rich, food items such as crustaceans. Although less available than sessile bivalves, species like *S. entomon* contain twice as much energy per unit wet weight as *M. edulis* (Rumohr et al. 1987); therefore, birds require less biomass to satisfy bioenergetic requirements.

Dominant prey of Long-tailed Ducks varies in different parts of the wintering range: gastropods are the predominant food item along the coasts of New Hampshire (Stott and Olson 1973) and northern Norway (Bustnes and Systad 2001); crustaceans are the most important prey for birds wintering at Lake Michigan (Peterson and Ellarson 1977), coastal British Columbia (Vermeer and Levings 1977), and Hudson Bay (Jamieson et al. 2001); and bivalves dominate their diet in the Baltic Sea (Madsen 1954, Nilsson 1972, Stempniewicz 1995, Kube 1996). Many authors agree that Long-tailed Ducks are opportunistic feeders, foraging on the most abundant and available prey (Peterson and Ellarson 1977, Goudie and Ankney 1986, Bustnes and Systad 2001). However, Jamieson et al. (2001) reported selective foraging by Long-tailed Ducks in polynyas (areas of open water in sea ice) of Hudson Bay, where birds fed almost exclusively on crustaceans, even though *M. edulis* were present. Jamieson et al. (2001) suggested that birds have to be selective by foraging on prey more profitable than *M. edulis* to meet energetic requirements in this harsh environment. Although bivalves generally dominate the diet of Long-tailed Ducks in the Baltic Sea, Stempniewicz (1995) found that males, which foraged at depths >20 m in the Gulf of Gdansk, fed exclusively on *S. entomon* isopods and suggested that only larger males are able to dive and feed efficiently at greater depths.

Assuming that animals attempt to maximize their net rate of energy intake by balancing food-item profitability and time spent feeding, the findings of our study can be discussed within the context optimal foraging theory (Pyke et al. 1977). If we assume that the rate of avian energy intake corresponds to the total biomass of macrozoobenthos, then Long-tailed Ducks would be expected to feed only in hard-bottom habitats where prey are abun-

dant and predictable. This theory is partly in agreement with our results, as we found a majority of Long-tailed Ducks occurring in rich, hard-bottom habitats. However some birds still used poor, soft-bottom areas and alternative explanations must be considered. Risk-sensitive foraging theory (Caraco 1980, 1981) may explain body condition of birds. This theory suggests that animals might make decisions to optimize a trade-off between food predictability in one habitat and greater maximum potential return in another (Caraco 1980, 1981). Guillemette et al. (1992) found that Common Eiders (*Somateria mollissima*) in good physiological condition in the Gulf of St. Lawrence used predictable habitats, where they foraged on blue mussels (*M. edulis*). Individuals in poorer condition, however, used a risk-prone foraging strategy and searched for more nutritious spider crabs (*Hyas araneus*) in habitat where prey abundance was low.

In our study area, Long-tailed Ducks used both productive hard-bottom habitat and areas with a relatively unproductive soft-bottom community. Risk-sensitive foraging theory (Caraco 1980, 1981) suggests that a nonselective foraging strategy among birds might be expected in rich, benthic communities, whereas an active searching strategy for particular food items might be employed in less productive habitats. Accordingly, Long-tailed Ducks foraging in rich, benthic communities should be in better physiological condition. Those in soft-bottom habitats should be in poorer or more variable condition. However, similar body conditions and variance estimates of Long-tailed Duck fat reserves in the two habitats indicate that Long-tailed Ducks—despite differences in productivity, foraging strategy, and food objects ingested—were able to attain similar (good) body condition. We speculate that the stable, and perhaps optimal, body reserves observed in Long-tailed Ducks throughout the wintering season indicate that birds are not energy stressed. Lower fat reserves in adult males may be due to higher energy expenditures during intensive courtship activities (RŽ pers. obs.) and/or better adaptability of males to the environment and a subsequent lower need to carry extra reserves.

The results of our study corroborate the

ecological plasticity of Long-tailed Ducks when selecting wintering habitats and choosing food items. We conclude that the majority of Long-tailed Ducks wintering in our study area actively select habitats and rely on the bivalve *M. edulis*. However, some of the population occurs in less productive habitats where they gain sufficient energy by foraging selectively on crustaceans.

#### ACKNOWLEDGMENTS

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## BREEDING BIOLOGY OF JABIRUS (*JABIRU MYCTERIA*) IN BELIZE

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**ABSTRACT.**—We summarized published and unpublished information on the reproductive biology and ecology of Jabirus (*Jabiru mycteria*) in Belize. From 1968 to 1987, 91 individual nests were discovered in 16 of 19 breeding seasons; 69 nests were confirmed as active. Jabiru nests were 15–30 m above ground in *Ceiba pentandra* (five nests), *Pinus caribaea* (five nests), *Tabebuia ochracea* (one nest), *Acoclorrhapha wrightii* (one nest), and dead trees (three nests). Most nests (32 of 36) were located in northern and central Belize in isolated, tall, emergent trees (trees with crowns that stand above the surrounding canopy). Nest trees were usually surrounded by riparian forests or seasonally inundated pine-savanna wetlands situated in transitional zones where pine savannah meets coastal lowlands. Two nests were used for at least 10 years. The breeding season began with the transition from wet to dry season (November–December). Earliest eggs were observed on 12 December 1973 and latest eggs on 26 February 1987. Earliest nestlings were observed on 15 January 1970, and young were seen on nests as late as 28 May 1973. Young birds fledged 100 to 115 days after hatching but were still dependent on parents. From 1968 to 1987, a total of 44 eggs and 92 nestlings were counted. Mean clutch size was  $3.14 \pm 1.17$  SE (range = 1–5 eggs,  $n = 14$  nests). Hatching success for four nests during the 1972–1973 breeding season was 43.8%. For 14 years in which crude hatching success (nestlings per active nest) could be calculated, 71.6% (43 of 60) of all active nests had at least one nestling. The mean number of nestlings per nest was  $2.13 \pm 0.71$  SE (range = 1–4 nestlings,  $n = 43$  nests). Productivity (the number of nestlings per nest for all active nests) was 1.53. These results were similar to those of two other studies of Jabiru breeding biology conducted in Brazil and Venezuela. Jabiru populations in Belize appear to have increased since the species gained protected status in 1973. Received 23 July 2004, accepted 4 March 2005.

Jabirus (*Jabiru mycteria*) breed locally from southern Mexico (Campeche, Tabasco) through the lowlands of Central America and east of the Andes to northern Argentina (Bent 1926, Blake 1977, Knoder et al. 1980, Hancock et al. 1992, Antas and Nascimento 1997). They favor extensive inland and shallow wetland habitats for feeding, but prefer nearby wooded areas for roosting and nesting (Hancock et al. 1992, Stotz et al. 1996, Antas and Nascimento 1997; DW pers. obs.). Jabirus are distributed widely but are not abundant anywhere in their breeding range. They are considered regionally threatened, although not endangered (Luthin 1984, 1987; Stotz et al. 1996). In southeastern Brazil, however, they have been extirpated from the basins of the Paraíba do Sul, Tietê, and Grande rivers, and there are only a few remnant populations restricted to the São Francisco River valley in

the state of Minas Gerais (Antas and Nascimento 1997:17).

Comprehensive information on numbers and population trends of Jabirus are limited, especially in Central America. Luthin (1987), however, observed Jabirus throughout their breeding range and concluded that there are three distinct populations: Central American, northern South American, and south-central South American. He suggested that research on the ecology and status of Jabirus be undertaken for each distinct population to develop a global conservation strategy for the species. DW (*in* Scott and Carbonell 1986) reported on the status of wetlands and conservation of waterbirds in Belize, referencing known Jabiru nesting areas. Recently, Frederick et al. (1997) documented previously unrecorded populations of Jabirus breeding in coastal wetlands of Nicaragua and Honduras, (Miskito Coast and La Mosquitia, respectively) during aerial strip-censuses of breeding waterbirds.

Kahl (1971, 1973), Thomas (1981, 1985), and Poveda (2003) described behavior and comparative ethology of Jabirus in Argentina, Venezuela, and Costa Rica, respectively, and Antas and Nascimento (1997) studied the

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TABLE 1. Observed egg-laying dates for the Jabiru, throughout its range.

Country	Egg-laying dates	Source
SE Mexico	Dec–Jan, Mar	Luthin 1984, Hancock et al. 1992
Belize	Dec–Feb	Hancock et al. 1992, this study
Honduras	Feb	Frederick et al. 1997
Nicaragua	Mar	Frederick et al. 1997
Costa Rica	Nov–Apr <sup>a</sup>	Villarreal-Orias 1988, Poveda 2003
Colombia (Rio San Jorge)	Sep–Nov	Kahl 1971, Hancock et al. 1992
Venezuela (Llanos)	Aug–Nov	Thomas 1985, González 1996a
Surinam	Aug–Oct	Spaans 1975, Hancock et al. 1992
Guyana	Aug–Oct	Hancock et al. 1992
E Brazil (Isla Mexiana)	Jul–Aug	Hancock et al. 1992, Antas and Nascimento 1997
SW Brazil (Mato Grosso)	Sep–Nov	Hancock et al. 1992, Antas and Nascimento 1997
Bolivia	Oct–Feb <sup>a</sup>	Dott 1984
NE Argentina (Corrientes, Chaco)	Aug–Oct	Kahl 1971, Hancock et al. 1992

<sup>a</sup> Breeding dates only; no egg-laying dates given.

ecology of Jabirus on the Pantanal of Brazil. Breeding and egg-laying dates have been published for some populations of Jabirus (Table 1). Breeding dates are variable across the range and seem to be influenced largely by seasonal rainfall patterns. Two published reports provide quantitative data on Jabiru breeding biology: González (1996a) and Anas and Nascimento (1997) for Venezuela and Brazil, respectively.

In Belize, the Belize Audubon Society (BAS) has published much anecdotal information on Jabiru nesting and sightings since 1969, but no comprehensive report exists for its breeding biology. From 1969 to 1987, DW and the late WFY collected information on nest locations and breeding activities of Jabirus in Belize, where the species has been officially protected since 1973. Our objective was to synthesize published and unpublished information from reliable sources and compile representative data for Jabirus in Belize. We then present an analysis of the breeding biology of Jabirus in Belize based on those sources.

## METHODS

*Study area.*—Most Jabiru nests for our study were located in the northern and central sections of Belize (17° 10'–18° 10' N; 89° 15'–88° 12' W; Fig. 1). Mean monthly temperatures range from 16 to 17° C in the winter wet season and from 24 to 25° C in the summer dry season. On average, the northern coastal plains (Corozal District) receive about one-

third the rainfall (1,347 mm) of the south (4,526 mm, Toledo District). Seasonal effects are greatest in the central and northern regions, where January through April or May are dry (<100 mm per month). In south-central regions, the dry season (February to April) is shorter. A minor, less rainy period usually occurs in August (Hartshorn et al. 1984, Central Statistical Office 2000).

*Data sources.*—Data for this study were gathered from four main sources: the unpublished field notes of DW (1968–1987), personal communications with DW from 2001 to 2003, 44 reports published in the Belize Audubon Society Bulletin from 1969 through 1987, and several letters written by WFY to Charles S. Luthin summarizing the results of nine census flights conducted between 1985 and 1986. C. S. Luthin worked for the Brehm Fund for International Bird Conservation and was chairman of the World Working Group on Storks, Ibises, and Spoonbills (WWG-SIS). We also included several recent 2003 personal observations from Belizean ornithologist, O. A. Figueroa.

Jabiru survey flights can be divided into two time periods: 1968–1981 and 1983–1987 (Table 2). Between 1968 and 1981, we confirmed 30 flights (~22.0 hr) by WFY (Young 1998). Flights were conducted in a single-engine aircraft and based out of Belize City Municipal Airport. These were low-altitude flights, often below 800 m, when nest contents were being observed. Nest locations (Appendix, Fig. 1) are approximate. To locate nest

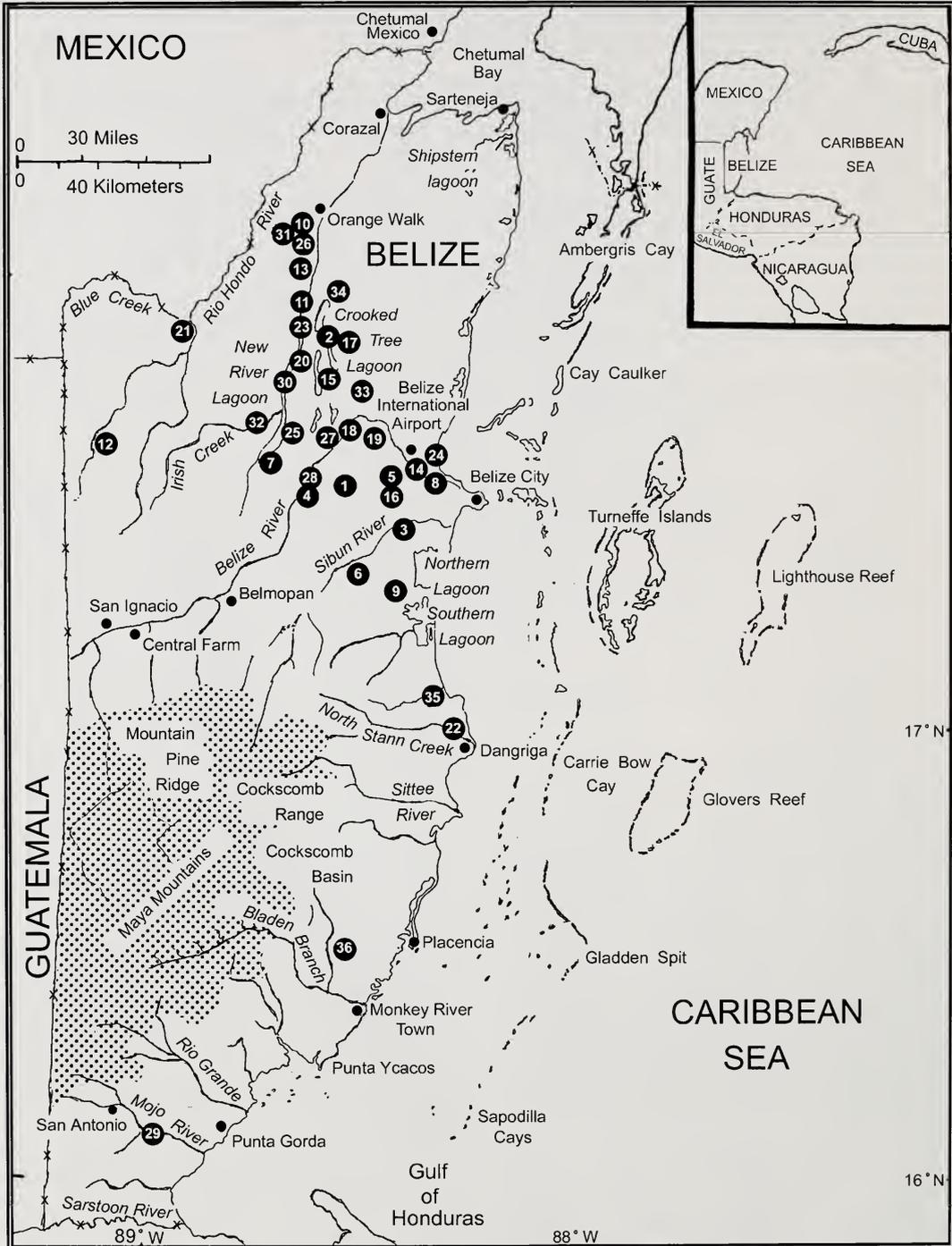


FIG. 1. Locations of 36 Jabiru nests in Belize, 1968–1987. Numbers on map refer to nesting sites listed in Appendix.

TABLE 2. Known flight dates for Jabiru surveys, 1968 to 1987<sup>a</sup>, Belize.

Season	Flight dates
1968–1969	Mar—no specific dates reported
1969–1970	15 Nov, Dec—no specific dates reported, 15 Mar
1970–1972	No flights confirmed
1972–1973	24 Jan, 26 Jan, 2 Feb, 27 Mar
1973–1974	23 Nov, 24 Nov, 27 Nov, 6 Jan, 17 May
1974–1975	12 Nov, 16 Nov, 23 Dec, 30 Mar, 30 Apr
1975–1976	2 Dec, 22 Dec, 26 Jan, 4 Mar
1976–1977	7 Dec, 22 Dec, 26 Jan, 4 Mar
1977–1978	No flights confirmed
1978–1979	Four flights—no specific dates reported
1979–1981	Various flights—no specific dates reported
1981–1983	No flights confirmed
1983–1984 <sup>b</sup>	25 Feb, 29 Apr—two flights each day
1984–1985 <sup>c</sup>	30 Jan, 31 Mar, 16 Apr, 11 May, 9 Jun, 23 Jun
1985–1986 <sup>d</sup>	17 Mar—two flights
1986–1987 <sup>e</sup>	26 Feb, 3 Mar, 8 Mar, 13 Mar, 29 Mar

<sup>a</sup> Total flight time ~22.0 hr, 1968–1981.

<sup>b</sup> Total flight time = 11.6 hr.

<sup>c</sup> Total flight time = 8.95 hr.

<sup>d</sup> Total flight time = 6.0 hr.

<sup>e</sup> No flight times reported.

sites, we referred to the aerial-flight (Fig. 2) and nest-location maps developed by WFY and DW from the WWG-SIS flights (1983–1986) and DW's notes. WFY had become personally interested in Jabirus and periodically took flights to confirm nest sightings reported by charter pilots and the public. He also owned a real estate business and often located nests when flying clients. Flights between 1969 and 1981 that were not real-estate related were highly targeted and covered central and northern Belize almost exclusively. After Jabirus gained protected status in 1973, public radio announcements were made to increase awareness and to encourage reports of nest sightings and Jabirus to the BAS. Flights that were conducted between 1968 and 1982 were systematic, in that they covered areas and habitats where previous sightings had been reported.

From 1983 to 1987, 12 of 15 flights (26.6 hr) were financed by WWG-SIS and flown by J. Fuller in a Cessna 172, V3-HEJ. These flights covered predetermined routes (Fig. 2), but also included some point-to-point trapline flights within the delineated area. Flight dates for annual nest surveys between 1968 and 1987 are given in Table 2. No regular flights were documented in BAS reports for surveys before 1984.

Most flights were between November and June. Nests were most detectable early in the season when at least one adult was incubating eggs or attending young birds. Observers who often participated in these early flights were BAS members DW, M. Meadows, and B. Miller; flights after 1984 also included J. Carnegie, J. Waight, and C. S. Luthin. Observers scanned from both sides of the aircraft. They looked for nests that were known to exist in previous years and for nests reported by charter pilots and the public. When a nest was detected, the pilot would circle around the nest at lower altitude, often at only 100 m, so that observers could see nest contents with binoculars. When an adult Jabiru was sitting on a nest, the aircraft would circle until the bird stood up and allowed a clear view of nest contents. Nest size was estimated by comparing it to the size of an adult Jabiru. Nest-size estimates were made from both aircraft and vantage points on the ground. Data were available for 16 breeding seasons; no data were available for 1970–1972, 1981–1982, or 1982–1983. Flying in Belizean airspace was severely restricted during the latter two breeding seasons due to a military conflict with Guatemala.

*Data analysis.*—To calculate reproductive success, data were considered reliable if they

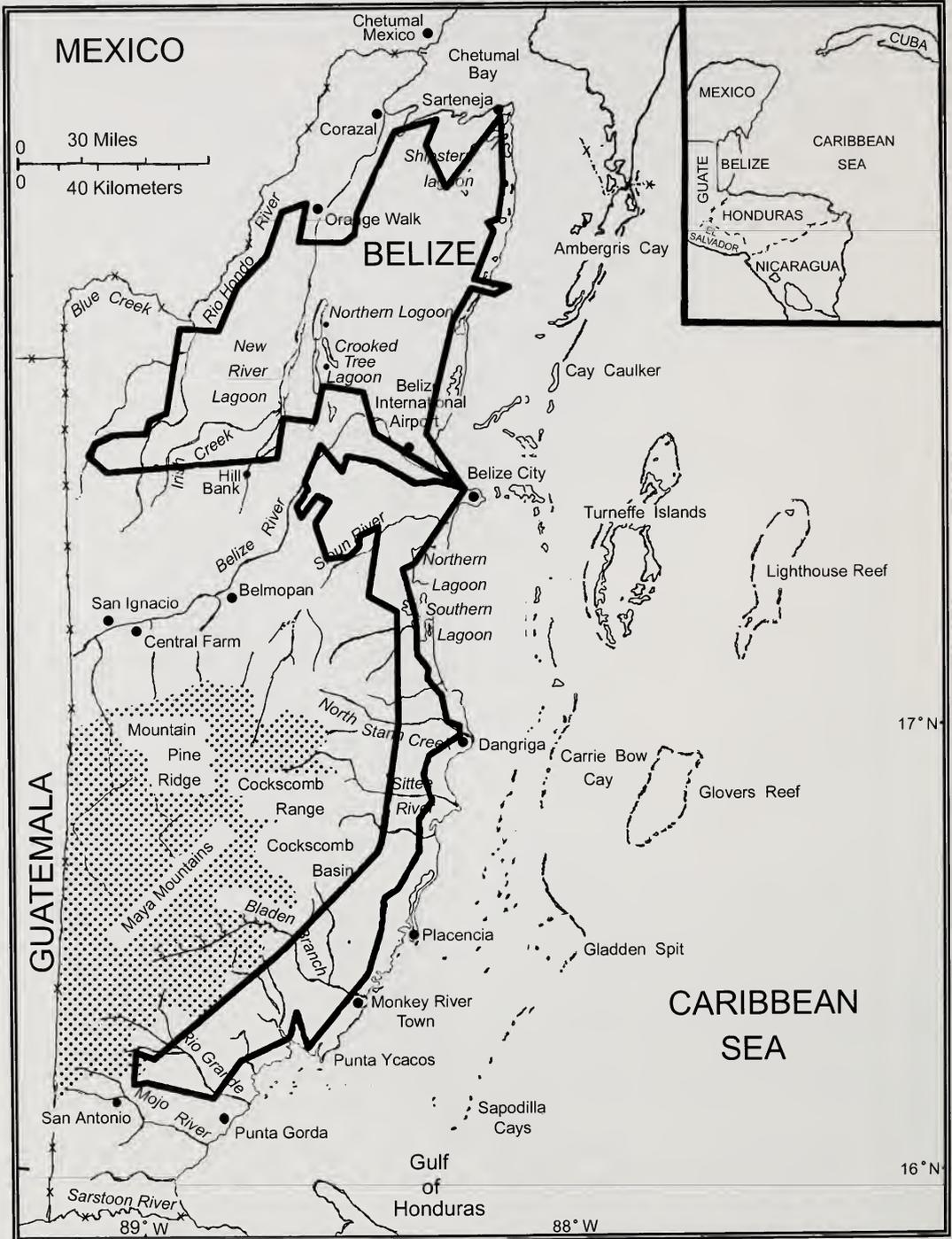


FIG. 2. Designated census routes for Jabiru nest survey flights in Belize, 1984–1987.

could be cross-referenced with BAS reports, DW's field notes, or WFY's letters. Where these data exist for breeding seasons 1968/1969 to 1986/1987, we have calculated total number of nests, active nests, eggs, nestlings, and mean clutch size. We calculated mean number of nestlings per nest for those nests with nestlings. Productivity was calculated as total number of nestlings per active nest (including nests with and without nestlings). Nests were considered to be active if adults appeared to be incubating, or if eggs or nestlings were observed in the nests. The number of young that successfully fledged could not be determined because nests were not monitored to fledging stage. Data represent the number of nestlings present at the nest.

For the 1972–1973 breeding season, we were able to calculate number of eggs that hatched (hatching success) for four nests. A crude measure of overall hatching success (1968–1987) was calculated by dividing number of nests where nestlings were observed by number of known active nests. In some years, nest data are missing; in other years, the number of nestlings observed contradicts the total number of nestlings reported by BAS, which may refer to the estimated number of young that fledged. Nest sites that could not be confirmed as either active or inactive were not included in our analysis.

## RESULTS

*Nest observations.*—A total of 144 nest observations were made in 16 breeding seasons: 121 (84%) from aircraft and 23 (16%) from the ground. The number of observations from the ground ranged from 1 to 7 per nest and the number of observations by aircraft ranged from 1 to 16. The mean number of observations per active nest was 2.4.

*Breeding behavior.*—Jabirus appeared to become more numerous in Belize near the end of the rainy season (mid-November), possibly having moved from the Campeche area of Mexico (Young 1983, Miller 1991). Both males and females appear to participate in nest building, incubation, and care of young (DW pers. obs., O. A. Figueroa pers. obs.).

During both incubation and when nestlings were present, one adult often remained on the nest while the other foraged (DW pers. obs.). Defense of nests against predators or other

bird species was not observed. However, breeding pairs appeared to remain in isolated breeding territories until nestlings fledged (DW pers. obs.). Jabirus may exhibit intra- and interspecific territoriality near the nest and at feeding areas (Hancock et al. 1992, González 1996b). When nestlings are about 4 weeks old, parents tend to leave them unattended for longer periods of time (O. A. Figueroa pers. obs.).

*Breeding dates.*—In Belize, the breeding season appears to coincide with the transition from wet to dry season (November–December). Most breeding occurs from mid-December to May. Recent observations indicate that a few nests are still active in early June (O. A. Figueroa pers. obs.). Most eggs are probably laid from December to February. Eggs seen in nests in February may have been laid during late January. Adults were observed standing on, constructing, or rebuilding nests as early as 16 November 1974. Earliest eggs were observed on 12 December 1973 and latest eggs were observed on 26 February 1987. Earliest nestlings were observed on 15 January 1970, and nestlings were observed as late as 28 May 1973. Young birds usually fledged 100–115 days after hatching (Miller 1991; DW pers. obs.), although some young fledge prior to 100 days post-hatching (O. A. Figueroa pers. obs.). Prior to finally abandoning the nest, young forage with their parents and continue to use the nest to roost. Successful Jabiru pairs are therefore involved in reproductive tasks for approximately 6–7 months.

*Nest sites.*—From 1968 to 1987, a total of 91 nests was discovered, of which 36 different nests were considered active in one or more years (Table 3, Appendix, Fig. 1). Each had at least one nesting attempt, yielding a total of 69 active nests over the course of 19 breeding seasons (Table 3). During the 1972–1973 breeding season, there were nine active nests and in 1986–1987 there were seven, but in most years there were five or fewer. All nests were in isolated, tall, emergent trees with one exception (Hattieville-Boom No. 1); this nest was constructed in an unusually tall group of palmetto palms (*Acoelorrhaphes wrightii*; Appendix, Fig. 1). Canopy height ranged from 10 to 30 m. We were able to identify the species of nest substrate for 12 of the 36 nests: *Ceiba pentandra* (5), *Pinus car-*

TABLE 3. Reproductive success of *Jabirus* in Belize during 1968–1987 breeding seasons.

Season	1968–1969	1969–1970	1970–1971	1971–1972	1972–1973	1973–1974	1974–1975	1975–1976
Total nests <sup>a</sup>	2	4	4	—	9	9	8	8
Active nests <sup>b</sup>	2	3	2	—	9	5	5	6
Nests with eggs	2	3	2	—	6	4	3	3
Mean clutch size	—	—	—	—	4.0 (4) <sup>d</sup>	2.5 (2)	5.0 (1)	3.0 (1)
Nests with young	2	3	2	—	7	2	3 <sup>e</sup>	1
Mean no. young	2.0 (2) <sup>f</sup>	2.0 (3)	2.0 (2)	—	2.1 (7)	1.5 (2)	2.0 (3) <sup>e</sup>	2.0 (1)
Total young	4	6	4	—	15	3	6	2
Hatching success (%)	—	—	—	—	43.8	—	—	—
Crude hatching success	100	100	100	—	78	40	44 <sup>g</sup>	16

<sup>a</sup> Total nests: active or inactive.

<sup>b</sup> Nests with eggs, nestlings, or incubating adults.

<sup>c</sup> These nests were not considered when calculating crude hatching success because no nestlings were observed in them.

<sup>d</sup> Number of nests where clutches were counted.

<sup>e</sup> Two of three nests were considered when calculating crude hatching success (the third nest was poached).

<sup>f</sup> Number of nests where nestlings were counted.

<sup>g</sup> Three nests were counted with nestlings, but one nest was destroyed before chicks fledged (that nest was not included in the calculation).

*ibaea* (5), *Tabebuia ochracea* (1), and palmetto palm (1). Three nests were found in unidentified dead trees. Nest trees were usually surrounded by riparian forests or seasonally inundated pine-savanna wetlands situated in transitional zones where pine savannah meets coastal lowlands; often nest trees were within seasonally flooded or permanent freshwater lagoons. The many coastal and inland lagoons in north-central and coastal areas of Belize provide nesting and foraging habitats; however, no nests were observed in mangrove-dominated areas. All nests were >1 km from mixed colonies of other bird species or other *Jabiru* nests.

**Construction and structure of nests.**—December and January appear to be the months when most nests are refurbished or new ones are built. Nests were usually 15–30 m above ground and were well supported in tree crotches. Nests often appeared deeper than wide. Nests were up to 1 m wide and 1.8 m deep, but most nests were as wide as they were deep. Each nest consisted of various sizes of sticks and other woody debris (although, to avoid disturbing the birds, no one climbed the nest trees to examine nest structures closely). Nests were continually refurbished throughout the breeding season and remained relatively flat on top (DW pers. obs.).

Several nests appeared to be used for many years. The Mucklehany Lagoon nest was discovered in 1968 and was last reported active in 1979. Two hurricanes, Francelia in 1969 and Fifi in 1974, defoliated the nest tree. New

nests were subsequently built in the same tree. The Bocotora Pine Ridge nest discovered in 1973 was last reported active in 1984 (Appendix, Fig. 1).

**Clutch size.**—Available data from 1968 to 1987 indicated a total of 44 eggs in 14 nests. Mean clutch size was  $3.14 \pm 1.17$  SE (range = 1–5 eggs;  $n = 14$  nests). Most eggs were laid in January.

**Hatching and nesting success.**—Hatching success could be calculated only for the 1972–1973 breeding season. Four nests with eggs were visited again when young were present. Sixteen eggs produced 7 nestlings, resulting in a hatching success of 43.8%. For the 14 years that crude hatching success (nestlings per active nest) could be calculated, 71.7% (43 of 60) of all active nests had at least one nestling present. A total of 92 nestlings was counted in 60 active nests, or 1.53 nestlings per active nest. The mean number of nestlings per nest with nestlings was  $2.13 \pm 0.71$  SE (range = 1–4 nestlings;  $n = 43$  nests). Most young were observed in February and March.

## DISCUSSION

González (1996a) reported that mean clutch size of *Jabirus* in Venezuela was 3.4 eggs, somewhat higher than the mean of 3.14 that we calculated in Belize. In a separate report (Young 1983), WFY and DW reported a mean clutch size of 4.1 eggs (range = 3–5 eggs;  $n = 19$  nests) in Belize. In Brazil, Antas and Nascimento (1997) reported a clutch size of 3–4 eggs. Hatching success was calculated for

TABLE 3. Extended.

1976-1977	1977-1978	1978-1979	1979-1980	1980-1981	1981-1982	1982-1983	1983-1984	1984-1985	1985-1986	1986-1987	Totals
6	1	6	3	2	—	—	6	7	6	10	91
4	1	6 <sup>c</sup>	3 <sup>c</sup>	2	—	—	5	5	4	7	69 (60)
4	1	3	—	2	—	—	4	—	1	1	39
2.0 (2)	—	3.0 (1)	—	—	—	—	3.0 (1)	—	3.0 (1)	2.0 (1)	—
2	1	—	—	2	—	—	5	5	3	6	44 (43)
2.5 (5)	2.0 (1)	—	—	2.0 (2)	—	—	3.0 (5)	2.6 (5)	1.3 (3)	1.5 (6)	—
5	2	—	—	4	—	—	15	13	4	9	92
—	—	—	—	—	—	—	—	—	—	—	—
50	100	—	—	100	—	—	100	100	75	86	—

only one breeding season in Belize (43.8%) and, over a 14-year period, crude hatching success was 71.7%. Although no fledgling data were collected in Belize, 47.0 and 47.6% of active nests produced at least one chick to fledgling age for two separate years in Venezuela (González 1996a).

Overall productivity per nest was higher in Belize (1.53) compared with 0.94 and 1.00 for the 2 years in Venezuela reported by González (1996a); however, his productivity measure was based on young per active nest that fledged, so the figures are not directly comparable. The mean number of nestlings per active nest was approximately the same in Belize (2.13) as it was during both years in Venezuela (2.0 and 2.1). In Brazil, mean number of nestlings per nest varied from a peak of 1.05 in 1988 to a minimum of 0.16 in November of 1992 (Antas and Nascimento 1997). In a separate report (Young 1983), WFY and DW found mean nestlings per active nest to be 2.18 (range = 1-4;  $n = 22$  nests) in Belize.

Based on documented reports, the main causes of the nest failures in Belize were human disturbance and nest trees being cut down by poachers (6 nests). Other nest failures were due to nest trees falling (4 nests), agricultural clearing (4 nests), and fire (1 nest). No predation was observed. Before Jabirus were officially protected in 1973, they were called "market birds" and nestlings, in particular, were hunted and their meat sold in markets. Public reports of poaching increased after the influx of refugees from Guatemala began in the early 1980s (DW pers. comm.).

As is the case in Venezuela, the breeding season for Jabirus in Belize appears to coincide with the end of seasonal rainfall. In the llanos of Venezuela, Thomas (1985) reported

that breeding of Wood Storks (*Mycteria americana*), Maguari Storks (*Ciconia maguari*), and Jabirus can be understood only within the context of variations in both timing and quantity of rainfall. The breeding season began just before the rains ended (September-October in Venezuela and November-December in Belize). Jabiru breeding dates in the Pantanal of Brazil varied, but were generally between early July and mid-August, with young leaving nests between October and early December. Water levels begin to fall in the Pantanal plain in May and June. Variations were noted even within one drainage basin, Taquari, where nests in the higher-elevation areas were active earlier than nests located in lower areas of the basin (Antas and Nascimento 1997). Nestling productivity in Brazil was likely related to flood levels, as the two fish species most often fed to nestlings were found in small bodies of water during low-water periods. Many populations of storks, including Jabirus, respond to the seasonal rainfall (Campbell and Lack 1985). In Brazil, this seasonal variation is expressed as volume of rain falling at river headwaters and that falling on the plains surrounding the Pantanal. The distribution of rain during the season directly influences both the total flooded area and the speed at which water levels rise and fall (Antas and Nascimento 1997:103).

In north-central Belize, Crooked Tree Wildlife Sanctuary (CTWS), a complex of permanent and seasonal shallow, freshwater lagoons and marshes, is a critical area for migratory and non-migratory water birds, including Jabirus. Some lagoons regularly dry up by the end of the dry season (March to May). Other lagoons are as deep as 3 m and retain water year around. Most observations

indicated that by mid-June very few adult or juvenile Jabirus remained in Belize. At this time, Jabiru populations are reported to increase in the Usumacinta drainage in Mexico, where they may possibly overwinter until the next breeding season (Luthin 1984, 1987; Miller 1991; Howell and Webb 1995; DW pers. comm.); no studies have confirmed whether birds from Belize winter there. It is uncertain, but Jabirus may become more dispersed as rising water levels make major wetlands less attractive for foraging but create new foraging opportunities in more isolated areas.

Many species of storks exhibit regional movements. These are dispersal events, not true migration, and are probably related to both timing and quantity of rainfall (Campbell and Lack 1985, Thomas 1985). Jabirus begin appearing in Belize during November and December, possibly arriving from the Campeche area of Mexico (Luthin 1984, 1987; Miller 1991; Howell and Webb 1995; Frederick et al. 1997). Birds move to locations where surface water conditions appear to favor optimum feeding. In Belize, during March and April when most young have fledged, water in lagoons and marshes becomes locally concentrated. Availability of food may be the single, most important factor that regulates movements of most storks, including Jabirus. It may also influence breeding success. The lowest nestling productivity in Brazil was reported during years of lowest rain fall (Antas and Nascimento 1997). A second example is that seasonal rains dictate timing and nesting success of Wood Stork populations in Florida: up to one-half of the total Wood Stork population may not nest in years when water conditions do not provide adequate food (Campbell and Lack 1985).

The numbers of adult Jabirus aggregating in lagoons at the termination of each breeding season were always much greater than the numbers known to be nesting (DW pers. obs.). In 1969 when DW first began keeping records, she recorded a group of 14 Jabirus (composed mostly of adults) at Mexico Lagoon on mud flats in mid-May. The numbers of Jabirus congregating at CTWS has increased: 14 in May 1970; 17 in June 1971 (Weyer 1971); 23 in June 1985 (Waight 1986); and 27 in March 1987 (Craig 1987). In recent

years (Waight and Beveridge 1991) at CTWS and adjacent Western Lagoon, as many as 40 and 49 Jabirus were observed in May and June 1991, respectively. In late May 1993, 50 Jabirus were observed at Northern Lagoon within CTWS (Young 1998). These observations indicate that there may be more Jabirus nesting in Belize than we report, because all nests are not equally observable (i.e., nests located inside the crowns of live trees or in lower parts of dead trees surrounded by leafy trees). These "extra" birds may represent a non-breeding group, which may be characteristic of long-lived birds that do not become reproductively active before the age of 4 years. These Jabirus could constitute a significant percentage of the population (O. A. Figueroa pers. comm.).

Most nest trees (32 of 36) were located in wetlands of northern and central Belize (Appendix, Fig. 1). This includes those in marshes along the lower New River, Crooked Tree Lagoon, Burrell Creek Lagoon, Mussel Creek, Big Falls Rice Ranch, Cox's Lagoon, and Muckelhany Lagoon. At least three nest trees were located within 1–5 km of the international airport in Ladyville, and south of the Sibun River to Northern Lagoon and Southern (Manatee) Lagoon in the Peccary Hills. Other locations include Laguna Seca, Monkey River south to Punta Yecacos Lagoon, upper Mojo River, Aguacaliente Swamp, and Mafredi Lagoon in Toledo District. DW (*in* Scott and Carbonell 1986) provided general site descriptions and status of these wetlands.

In Belize, Jabirus built nests far from other wading-bird nests. They were never observed nesting in close proximity to Wood Storks and only once, in May 1978, was a colony of Boat-billed Herons (*Cochlearius cochlearius*) observed within a few hundred meters of a Jabiru nest at Blue Creek Village nest (Appendix, Fig. 1). DW's 1985 observations in the llanos of Venezuela (Masa Guaral) and Naumburg's (*in* Kahl 1971) observations in Mato Grosso, Brazil, indicated that Jabirus nested within colonies of Wood Storks and other Ciconiiformes. González (1996a) found three Jabiru nests in the center of mixed-species colonies in Venezuela. Luthin (1984) found one Jabiru nest in a mixed-species colony in Mexico. Some nests were built in tall red mangroves (*Rhizophora mangle*) in coastal

areas of southern Mexico. In Brazil, both sexes of Jabiru have been observed defending the nest and surrounding area from other Jabirus and Wood Storks (Antas and Nascimento 1997). Inter- and intraspecific kleptoparasitism was a very common behavior during the late dry season in the llanos of Venezuela (González 1996b), and Jabirus exhibited territoriality throughout the nesting season (Kahl 1973, Thomas 1985). In Belize, DW rarely observed behavior during the breeding season that she considered territorial defense of food resources. Beginning in April, small groups of mostly adult Jabirus congregated in freshwater marshes, ponds, and lagoons where food resources may have become concentrated during the dry season (DW pers. obs.) These areas were termed "staging" areas by DW, as very few Jabirus were observed during the non-breeding season in Belize. It is unknown—but suggested—that Jabiru populations of Central America may move seasonally between Mexico, Belize, and Guatemala (Correa and Luthin 1988; DW pers. comm.). Other reports (Ogden et al. 1988, Villarreal 1996) suggest that seasonal influxes may occur in various regions of Central America.

In Venezuela, González (1996a) reported that nestlings remained on nests from 84 to 93 days, but that fledglings remained near the nest for several weeks afterward, in many cases returning to the nest at night. In Belize, young birds remain in the nest or near the nest for 100–115 days. Successful Jabiru pairs in all three countries (Belize, Brazil, and Venezuela) are involved in reproductive tasks for approximately 7 months and may have difficulty breeding in successive years; there is, however, some evidence that Jabiru pairs may remain mated in successive seasons (Kahl 1973, Thomas 1985, González 1996a). González (1996a) indicates that less than half of all active pairs in one season are also active during the following season, and that only 25% of successful pairs are successful in a second consecutive season.

Overall, Jabiru populations may have increased in Belize since gaining protective status in 1973. In the early 1970s, the Belize Audubon Society had estimated the population to be 20–30 birds, but by 1993, the population was estimated to be 50–60 birds (Young 1998). By 2002, 102 Jabirus had been counted

in the major wetlands of Belize (O. A. Figueroa pers. comm.).

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APPENDIX. Jabiru nest numbers, names, and first breeding season discovered in Belize, 1968–1987. Numbers refer to locations shown in Figure 1.

Nest No.	Nest name	Season discovered
1	Mucklehany Lagoon	1968–1969
2	Northern Lagoon	1968–1969
3	Hattieville	1969–1970
4	Mason's Farm/Cabbage Haul Swamp	1969–1970
5	Hattieville–Boom No. 1	1970–1971
6	Sibun River	1972–1973
7	Hill Bank at Dawson Creek	1972–1973
8	Perry Camp No. 1	1972–1973
9	Bocotora Pine Ridge	1972–1973
10	Orange Walk Town No. 1	1972–1973
11	Ship Yard Village	1972–1973
12	Laguna Seca	1972–1973
13	Guinea Grass	1973–1974
14	Perry Camp No. 2	1973–1974
15	Spanish Creek and Southern Lagoon	1973–1974
16	Hattieville Boom No. 2	1975–1976
17	Mexico Lagoon	1975–1976
18	Isabella Bank	1975–1976
19	Burrel Boom (Tenn Ag)	1975–1976
20	Dawson Creek	1986–1987
21	Blue Creek Village	1977–1978
22	Dandriga Nest	1978–1979
23	Back Landing	1978–1979
24	International Airport	1979–1980
25	Lemonal Nest	1979–1980
26	Orange Walk No. 2	1983–1984
27	Spanish Creek	1983–1984
28	Double Headed Cabbage	1983–1984
29	Mojo Swamp	1983–1984
30	Indian Church	1985–1986
31	San Antonio Village	1983–1984
32	Irish Creek	1986–1987
33	Black Creek House	1986–1987
34	Revenge Lagoon	1986–1987
35	Mullins River	1986–1987
36	Mango Farm–Monkey River	1986–1987

## ABUNDANCE, HABITAT USE, AND MOVEMENTS OF BLUE-WINGED MACAWS (*PRIMOLIUS MARACANA*) AND OTHER PARROTS IN AND AROUND AN ATLANTIC FOREST RESERVE

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**ABSTRACT.**—The Blue-winged Macaw (*Primolius maracana*) has disappeared from most of southern Brazil, Argentina, and Paraguay; its remaining southern stronghold is the 2,179-ha Caetetus Reserve, São Paulo state, Brazil. We estimated the macaw's population inside the reserve (88 individuals) and examined how it and other parrots use the extra-reserve landscape, which is dominated by coffee plantations and pasturelands. Flight activity of the macaw and Scaly-headed Parrot (*Pionus maximiliani*) declined with distance from Caetetus, although many macaws flew to the vicinity of the reserve to roost. Two other species, Canary-winged Parakeet (*Brotogeris versicolurus*) and White-eyed Parakeet (*Aratinga leucophthalmus*), used the landscape independent of the reserve itself. We recorded parrots in 90% of our 1-km<sup>2</sup> study plots outside (<12 km) the reserve, but no species was recorded using pasture, coffee or rubber/orange plantations, or scrub habitats, which composed 80% of the landscape around the reserve. Only four habitat types were used by any species. Primary and secondary forests were the habitats most preferred; *Eucalyptus* plantation habitat was the only totally anthropogenic habitat used. Clearly, protection, and preferably augmentation, of forest cover around Caetetus may be crucial for the macaw's survival at this important site. Received 2 March 2004, accepted 11 January 2005.

Habitat fragmentation has affected a multitude of taxa worldwide (e.g., Saunders et al. 1991, Turner 1996) by disrupting forest dynamics (Laurance et al. 1998) and adversely affecting floras and faunas (Alzen and Feinsinger 1994, Dale et al. 1994). Surprisingly, few studies have examined the effects of fragmentation on large frugivorous birds such as parrots, hornbills, and toucans. These birds are among the most threatened in the world (BirdLife International 2000) and often disappear from small fragments (e.g., Willis 1979). On the other hand, many are also highly mobile, which may allow them to disperse to areas within fragmented landscapes (e.g., Rowley 1983, McNally and Horrocks 2000).

The ability of a given species to use the mosaic of different habitats found outside of reserves (extra-reserve landscape) may affect its future survival, which makes this an important topic for research. Agro-ecosystems cover the vast majority of land outside protected areas (Western and Pearl 1989), which could have important influences on species ecology (Mesquita et al. 1999, Bentley et al.

2000) and survival (Laurance 1991, Gascon et al. 1999). A species' ability to use the extra-reserve landscape may be especially important around protected areas or other habitat fragments, as dispersal into the extra-reserve landscape might boost local populations (e.g., Ricketts et al. 2000). In the case of large avian frugivores, which tend to occur at low population densities (e.g., Marsden 1999), it is unknown whether protected areas can support viable populations of some taxa, especially in small reserves (e.g., Gurd et al. 2001). Examination of landscapes adjacent to reserves or other "key patches" (Verboom et al. 2001), and improving extra-reserve habitat suitability for threatened taxa, may be a first step toward enhancing populations in and around protected areas, or at least buffering within-reserve populations from negative outside influences (e.g., Gotmark et al. 2000).

The problem of forest fragmentation is acute in Brazil's Atlantic Forest, where remaining forest cover is ~7.5% of the original 1 million km<sup>2</sup> (Morellato and Haddad 2000, Myers et al. 2000). Deforestation has been particularly intense in the interior of São Paulo state; aside from the relatively large Morro do Diabo State Park, the few small fragments of forest that remain are isolated by vast areas of sugar cane and other agricultural land (e.g., Cullen et al. 2001). One of these fragments is

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the Caetetus Reserve (2,179 ha), situated near Garça. The reserve is surrounded by an extra-reserve landscape dominated by pasturelands and coffee plantations, but which also contains small areas of remnant and degraded forest, along with plantations of *Eucalyptus* spp. and citrus fruits. The reserve holds São Paulo's largest remaining population of the Blue-winged Macaw (*Primolius maracana*; formerly placed within *Ara* or *Propyrrhura* but now assigned to *Primolius*, Tavares et al. 2004), a species classified as "Vulnerable" (BirdLife International 2000). This species (body length = 39 cm) has disappeared from many of the protected areas in the southern part of its range (M. F. Nunes unpubl. data). Six other parrot species survive in the area (body lengths from Juniper and Parr 1998): White-eyed Parakeet (*Aratinga leucophthalmus*), 32 cm; Maroon-bellied Parakeet (*Pyrrhura frontalis*), 25–28 cm; Blue-winged Parrotlet (*Forpus xanthopterygius*), 12 cm; Canary-winged Parakeet (*Brotogeris versicolurus*), 25 cm; Scaly-headed Parrot (*Pionus maximiliani*), 27 cm; and Blue-fronted Parrot (*Amazona aestiva*), 37 cm.

Our objectives were to (1) estimate population sizes of Blue-winged Macaws and other parrot species within the reserve, (2) examine parrot use of the extra-reserve landscape, and (3) determine which features of the extra-reserve landscape influence parrot use. We then used these results to make a preliminary assessment of the likely viability of parrot populations in the area and to suggest which features of the landscape should be preserved or enhanced to protect parrots.

## METHODS

**Study area.**—The study was based in and around Caetetus Ecological Station, São Paulo state, Brazil (22° 24' S, 49° 42' W; Fig. 1). The reserve covers 2,179 ha and consists mainly of mature, semi-deciduous forest (the area has been protected from major logging for ~30 years) and some areas of more recently disturbed secondary forest. Additionally, there are much smaller areas dominated by stands of bamboo and palmito (*Euterpe edulis*), and some small artificial lakes (Fig. 1). Annual precipitation averages 1,260 mm (Cullen et al. 2001). The study was conducted toward the end of the dry, cool season (May to

September) in the plateau region of São Paulo. The landscape surrounding Caetetus is dominated by pasturelands and coffee plantations (Table 1), although fragments of degraded and regenerating forest and riverine forest also occur outside the reserve.

**Within-reserve study.**—We censused parrots in July and August 2001. The identification of parrot species, by both sight and call, and estimation of their distances from census points, was practiced for 10 days before starting the study. We established 90 parrot census points at 200-m intervals along nine transects. Caetetus has an existing network of narrow "research" trails covering much of the reserve and all points were placed along these trails (Fig. 1).

We sampled each census point six times—three times between 07:30 and 10:00 (UTC–03) and three times between 14:30 and 17:00—giving a total of 540 samples. Point counts commenced immediately upon reaching the point and lasted 5 min; any parrots observed close to the census point as the observer approached the station were also recorded. We recorded parrots within 50 m of the census point. For each parrot, we recorded the species, group size, whether it was flying or perched, the time it was seen or heard, and an estimate—or in some cases an actual measurement—of the distance from point to parrot.

Within a 40-m radius of each census point, we measured several habitat variables. We chose a 40-m rather than 50-m radius for ease of data collection and because only a small proportion of parrot records were expected at distances of 40–50 m away from the observer. We recorded the number of dead standing trees and the circumference at breast height of the five largest trees. Trees on which the first major branch was at or above half the tree's height were categorized as "primary-forest" trees, as they had probably grown under a full canopy. Trees branching below half their height, those with scars from dropped branches, or those showing vertical growth of branches near their base, were categorized as "secondary-forest" trees. The distance of each point to the nearest forest edge and the nearest river or lake was determined from Global Positioning System (GPS) coordinates and maps.

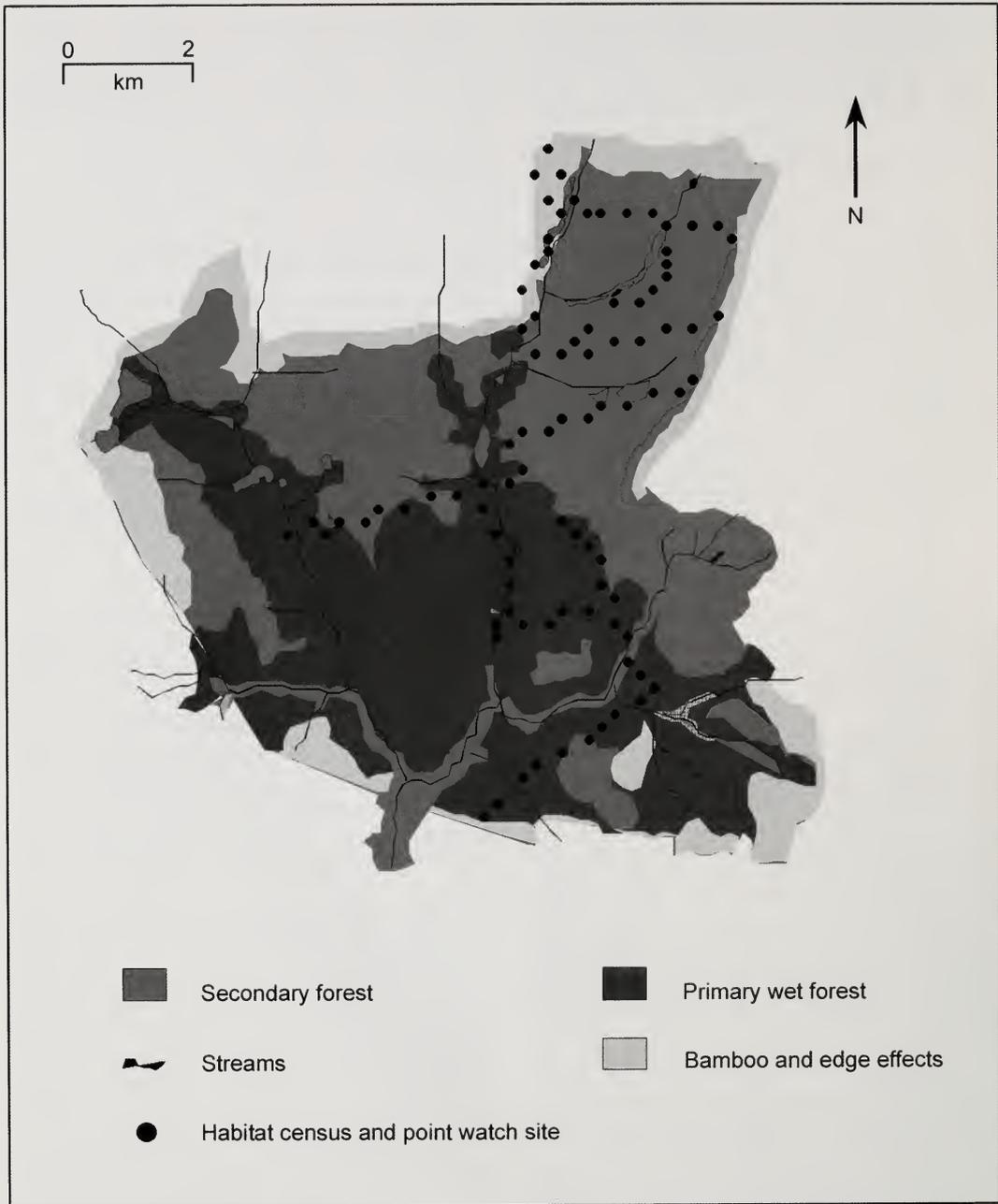


FIG. 1. Map of Caetetus Ecological Station, São Paulo state, Brazil, showing broad habitat types and census points within the reserve.

*Extra-reserve study.*—Habitat use and movements of parrots outside the reserve were studied in seventy 1- × 1-km plots located within a 12-km radius of the center of the Caetetus Reserve, thus composing 16.3% of

the extra-reserve landscape within the 12-km-radius circle (Fig. 2). Thirty-five study plots were chosen randomly, then each was paired with a second, adjacent plot. Each pair of plots thus composed a 1- × 2-km rectangle

TABLE 1. Percentage cover and main vegetation types of habitats found in the extra-reserve landscape around Caetetus Ecological Station, São Paulo state, Brazil (2002).

Habitat type	Percentage cover	Dominant vegetation/species
Pasture	42.0	Various grass species
Coffee plantation	33.0	<i>Coffea</i> spp.
Riverine forest	8.0	<i>Calophyllum brasiliensis</i>
Primary forest	6.0	<i>Peroba</i> spp., <i>Talauma ovata</i>
Secondary forest	4.5	<i>Gallesia</i> spp., <i>Cecropia</i> spp.
Scrub	2.9	<i>Ormosia arborea</i> , <i>Cecropia</i> spp.
<i>Eucalyptus</i> plantation	2.1	<i>Eucalyptus</i> spp.
Rubber/orange plantation	1.1	<i>Hevea brasiliensis</i> , <i>Citrus</i> spp.

with the long axis facing (i.e.,  $<45^\circ$  from) the nearest part of the reserve (Fig. 2).

During July and August 2001, parrot movements and habitat use in each plot were recorded (one observer per plot) during one day between 07:00 and 10:30 and again between 15:00 and 17:30. Observer position within a plot was determined by the best view afforded

of the plot (but all points were within 200 m of the plot's perimeter); because the landscape around Caetetus is gently rolling, it was possible to find points at which the view over each plot was practically complete. During each survey, we recorded the parrot species, group size, time of entry into the plot, flight direction, and type of habitat used.

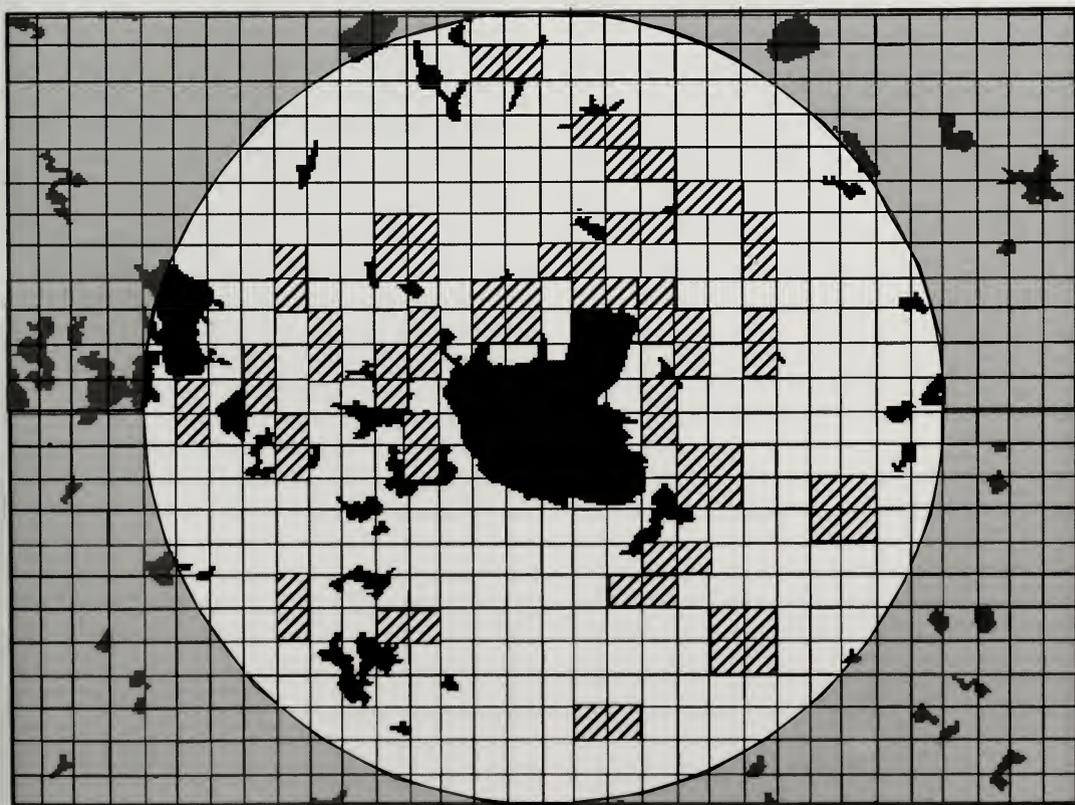


FIG. 2. The landscape around Caetetus Ecological Station, São Paulo state, Brazil. The circle represents the study area within 12 km of the center of the reserve. Also shown are 1- × 1-km study plots (hatched) and extra-reserve forest remnants (black). Areas in gray are outside the study area.

A vegetation survey was carried out in each square on the day of the parrot survey. Four 1,000-m transects were placed parallel to each other at 200, 400, 600, and 800 m across each plot, providing 4 km of transect per plot. One observer (BE) walked the transects, recording with a GPS the total length of each of 11 habitat types. Habitat types contributing >1% of total habitat measured are shown in Table 1; the other habitats were bamboo, marsh, and buildings. Natural forests were classified as primary forest if there was little evidence of disturbance and the canopy was closed (these areas were usually fenced off), or as secondary forest if there was evidence of much heavier disturbance (logging, fire, and grazing by cattle) and/or the canopy was discontinuous. We calculated a habitat-richness variable for each plot by summing the number of habitat types.

From digitized maps, we calculated three measures of connectivity between each plot and the Caetetus Reserve. Distance to the reserve (DIST) was calculated as the distance from the plot to the nearest edge of the reserve. Percentage of forested land between the plot and the reserve (FOREST) was calculated as the percentage of the DIST vector that transected natural forest (primary, secondary, or riverine forests). Finally, an index of forest gap (GAP) between the plot and the reserve was calculated as the greatest distance between adjacent areas of forest along the DIST vector, divided by DIST.

To determine whether extra-reserve habitats were geographically clumped (which could influence extra-reserve landscape use by parrots) and whether we could treat paired plots as independent of one another, we tested for spatial autocorrelation in habitat measures between paired plots. Specifically, we ascertained whether adjacent plots were more similar to each other than they were to randomly selected plots with respect to eight habitat/landscape variables: percent primary forest, secondary forest, scrub, pasture, coffee, and *Eucalyptus*, as well as DIST and FOREST. First, we calculated—for each variable—the difference between paired plots by subtracting the smaller value from the greater value. Second, we calculated this difference between one of the two original plots (randomly selected) and one of the other 68 plots (random-

ly selected). We then compared the paired and random differences using Wilcoxon signed ranks tests ( $n = 70$ ).

*Data analysis.*—Three parrot species—Maroon-bellied Parakeet, Blue-winged Parrotlet and Blue-fronted Parrot—composed only 1.2% of parrots recorded in the extra-reserve landscape and were excluded from data analysis. This left four species for analysis: Blue-winged Macaw, Scaly-headed Parrot, White-eyed Parakeet, and Canary-winged Parakeet. All four species were found outside the reserve, but only macaws and Scaly-headed Parrots were recorded at census points inside the reserve.

Habitat associations of parrots inside the reserve were examined by testing for differences between habitat/landscape variables at “positive” census stations (species present on any of the six surveys) and “negative” stations (species absent). We used independent  $t$ -tests for habitat variables that were normally distributed, and Mann-Whitney  $U$ -tests for those with non-normal distributions.

We used Program DISTANCE (Buckland et al. 2001) to calculate density estimates for the two species (Blue-winged Macaw and Scaly-headed Parrot) recorded in the reserve. Records were entered in clusters, and density estimates were based on mean group size unless size-bias regressions of group size against distance were significant at  $P < 0.10$ , in which case group size was adjusted by DISTANCE. Records of parrots in flight were excluded from the analysis, as aerial records clearly violate a key assumption of distance sampling (Marsden 1999). Data were converted to 4–5 bands for analysis. No right-hand truncation was used. Model selection and fit were assessed using the Akaike Information Criteria (AIC) minimization criterion and goodness-of-fit tests (Buckland et al. 2001). For both species, the pattern of detection best fit the uniform model with cosine adjustment. Density estimates were used in conjunction with the area of the reserve to produce estimates of total within-reserve population size.

To evaluate habitat use in the extra-reserve landscape, we analyzed records of birds in flight and records of birds that were perched. The flight direction of each bird in flight was classified as toward, away from, or parallel to the Caetetus Reserve. Chi-square tests were

TABLE 2. Positive (species present) and negative (species absent) habitat associations (mean  $\pm$  SE) of perched parrots in Caetetus Reserve, São Paulo state, Brazil (2002). Boldfaced values are significantly different after sequential Bonferroni adjustment (*t*-tests were used for normally distributed variables; otherwise Mann-Whitney *U*-tests were used).

Habitat parameter	<i>Primolius maracana</i>		<i>Pionus maximiliani</i>	
	Present <i>n</i> <sup>a</sup> = 8	Absent <i>n</i> <sup>a</sup> = 82	Present <i>n</i> <sup>a</sup> = 26	Absent <i>n</i> <sup>a</sup> = 64
Distance from edge (m)	769 $\pm$ 470	909 $\pm$ 484	760 $\pm$ 398	952 $\pm$ 504
Distance from water (m)	306 $\pm$ 186	293 $\pm$ 209	252 $\pm$ 175	311 $\pm$ 217
No. dead standing trees	<b>1.6 <math>\pm</math> 2.2</b>	<b>3.1 <math>\pm</math> 2<sup>b</sup></b>	2.9 $\pm$ 2.2	2.9 $\pm$ 1.9
No. primary forest trees	<b>4.6 <math>\pm</math> 0.7</b>	<b>3.5 <math>\pm</math> 1.4<sup>c</sup></b>	3.7 $\pm$ 1.4	3.6 $\pm$ 1.4
Tree circumference (cm)	116 $\pm$ 17	135 $\pm$ 46	130 $\pm$ 43	135 $\pm$ 45
Circumference of largest tree (cm)	174 $\pm$ 42	214 $\pm$ 95	194 $\pm$ 90	217 $\pm$ 92

<sup>a</sup> Number of point count stations.

<sup>b</sup> *P* = 0.039, Mann-Whitney *U*-test = 185.

<sup>c</sup> *P* = 0.016, Mann-Whitney *U*-test = 163.5.

used to examine differences in flight directions of each species during the mornings and afternoons. Diurnal patterns of flight activity and habitat use were assessed by plotting the mean numbers of each species flying or perched per hr per km<sup>2</sup> during each hour of the morning (07:00–10:00) and afternoon survey periods (15:30–17:30).

Spearman's rank analyses were used to identify correlations between pairs of species in terms of how they used the 70 plots. In all multiple comparisons, we used a sequential Bonferroni adjustment (Rice 1989) to determine significance of individual correlations. Spearman's rank analyses also were used to identify correlations between the amount of flight activity and extra-reserve habitat type, richness, and connectivity measures. In effect, we looked for correlations between the number of flights made by parrot groups per hour across plots and the habitat or connectivity characteristics of those plots (e.g., percentage cover of each habitat type, distance to reserve).

To calculate a habitat preference index for each parrot species, we compared the proportion of perched parrot records (whether singly or in groups) in a given habitat type to the total percentage of that habitat type. For example, if 10% of perched records of a species were recorded in a habitat that composed 10% of the total vegetation across all plots, then the index of usage would equal 1. Values  $>1$  indicated habitat selection, and  $<1$  indicated habitat avoidance. Zero indicated habitats never used.

## RESULTS

*Habitat use and abundance within the reserve.*—Although four parrot species were recorded in or flying over the reserve, *B. versicolurus* and *F. xanthopterygius* were only occasionally recorded. The two regularly recorded species, *P. maracana* and *P. maximiliani*, were neither positively nor negatively associated ( $\chi^2 = 0.02$ , *df* = 1, *P* = 0.88) with one another.

The presence of perched *P. maracana* at census points was negatively associated with the number of dead standing trees, and positively associated with the number of primary forest trees (Table 2). *P. maximiliani* showed no significant relationships with any of the habitat variables.

We recorded only 35 perched parrots during 540 point counts (*n* = 11 for *P. maracana*, and *n* = 24 for *P. maximiliani*). However, because these data represent only those parrots detected within 50 m of census points, density estimates were still reasonably high. The density estimate for *P. maximiliani* (8.8  $\pm$  2.0 per km<sup>2</sup>) was approximately twice that of *P. maracana* (4.1  $\pm$  1.6 per km<sup>2</sup>). The population estimate for *P. maracana* was 88  $\pm$  34 individuals (Table 3).

*The extra-reserve habitat and its use by parrots.*—Pasturelands and coffee plantations were the predominant habitat types, composing 75% of the extra-reserve landscape. Riverine and primary forests were the dominant natural habitats, but represented only 14% of the area. Natural habitats made up 21.4% of the extra-reserve landscape (Table 1).

TABLE 3. Encounter rates (groups encountered/10 point counts), density estimates (individuals/km<sup>2</sup>), and population estimates for parrots in Caetetus Reserve, São Paulo state, Brazil (2002). Values are means  $\pm$  SE (upper and lower 95% CI).

	<i>Primolius maracana</i>	<i>Pionus maximiliani</i>
Number of groups ( <i>n</i> )	11	24
Number of point counts ( <i>K</i> )	540	540
Encounter rate	0.20 $\pm$ 0.08	0.44 $\pm$ 0.10
Density estimate	4.1 $\pm$ 1.6 (1.9–8.5)	8.8 $\pm$ 2.0 (5.7–14)
Population estimate	88 $\pm$ 34 (42–185)	193 $\pm$ 44 (123–301)

*P. maracana* and *B. versicolorus* were the two most frequently recorded species (Table 4). Use of extra-reserve habitats by *P. maracana* was positively correlated with that of both *P. maximiliani* and *B. versicolorus*. Use of extra-reserve habitats by *B. versicolorus* was positively correlated with that of all other species.

Of the eight habitat/landscape variables tested, only DIST showed significant autocorrelation between plots ( $Z = 5.02$ ,  $P < 0.001$ ); this is not surprising, as adjacent plots were nearly equidistant from the reserve. Neither FOREST ( $Z = 0.60$ ,  $P = 0.55$ ) nor any of the habitat variables were autocorrelated: primary forest ( $Z = 1.50$ ,  $P = 0.13$ ), secondary forest ( $Z = 0.72$ ,  $P = 0.47$ ), scrub ( $Z = 0.36$ ,  $P = 0.72$ ), *Eucalyptus* ( $Z = 0.75$ ,  $P = 0.46$ ), coffee ( $Z = 1.41$ ,  $P = 0.16$ ), or pasture ( $Z = 1.8$ ,  $P = 0.072$ ).

*Extra-reserve activity and movements.*—Extra-reserve flight activity of *P. maracana* and *P. maximiliani* was greater in the mornings and evenings than during the middle of the day (Fig. 3A, B), whereas *B. versicolorus* exhibited greater flight activity in the early mornings (Fig. 3C). There were more records

of perched *P. maracana* early in the mornings (Fig. 3D), whereas perched *B. versicolorus* were recorded more often in the afternoons (Fig. 3F).

Direction of *P. maracana* flight (the number of groups flying toward, away from, or parallel to the reserve) differed between the morning and afternoon ( $\chi^2 = 29.2$ ,  $df = 2$ ,  $P < 0.001$ ). More birds flew away from the reserve in the morning, and more flew toward the reserve in the evenings than expected (numbers of parrots flying in other directions were similar in the mornings and evenings). There was no difference in the direction of morning and evening flights for *P. maximiliani* ( $\chi^2 = 0.77$ ,  $df = 2$ ,  $P = 0.68$ ) or for *B. versicolorus* ( $\chi^2 = 3.76$ ,  $df = 2$ ,  $P = 0.15$ ).

*Factors influencing parrot movements.*—Flight activity of *P. maracana* and *P. maximiliani* outside the reserve decreased with increasing DIST; however, none of the other connectivity variables were correlated with parrot movements (Table 5). Parrot groups of three species were recorded flying more frequently over plots containing relatively large percentages of natural habitats (primary, secondary and riverine forest, and scrub). Flight

TABLE 4. Parrot use of 1-  $\times$  1-km plots outside the Caetetus Reserve ( $n = 70$  plots in all cases), São Paulo state, Brazil (2002). Associations between species are based on Spearman's rank correlation analyses of abundance of perched groups within plots. Spearman's coefficients are given for significant ( $P < 0.05$ ) correlations after a sequential Bonferroni adjustment.

	No. groups		% 1- $\times$ 1-km plots		Correlations		
	F <sup>a</sup>	P <sup>a</sup>	F	P <sup>a</sup>	<i>Pionus maximiliani</i>	<i>Aratinga leucophthalmus</i>	<i>Brotogeris versicolorus</i>
<i>Primolius maracana</i>	249	41	86	27	+0.40	NS <sup>b</sup>	+0.50
<i>Pionus maximiliani</i>	142	25	44	16		NS <sup>b</sup>	+0.35
<i>Aratinga leucophthalmus</i>	9	15	7	4			+0.45
<i>Brotogeris versicolorus</i>	234	60	67	21			

<sup>a</sup> F = flying record, P = perched record.

<sup>b</sup> NS = not significant.

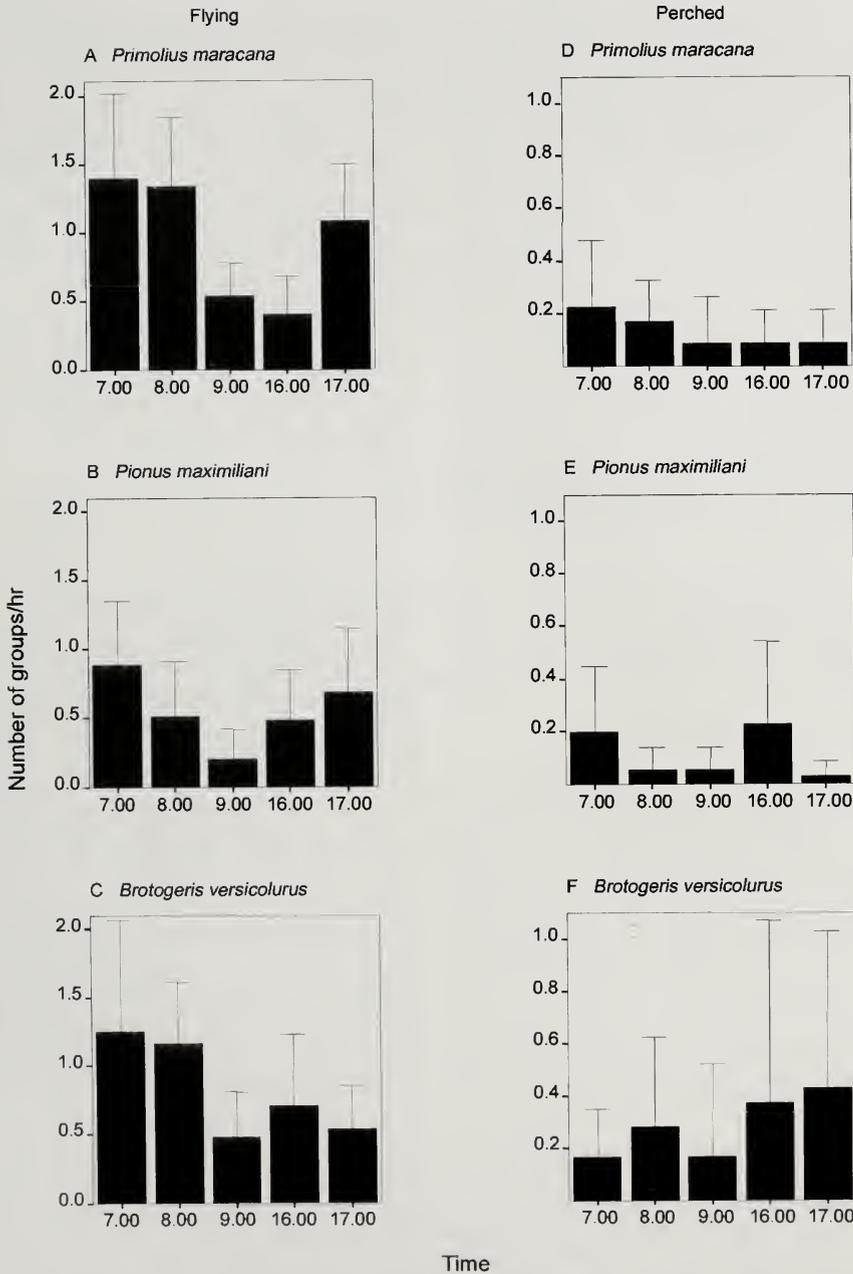


FIG. 3. Diurnal extra-reserve flight activity and habitat use (perched) for three commonly recorded parrot species at Caetetus Reserve, São Paulo state, Brazil. Bars represent the mean number of groups recorded per hour (mean ± SE) within hour-long time periods.

frequency of *A. leucophthalmus* was positively correlated with habitat richness within plots.

*Extra-reserve habitat use.*—Only four of the extra-reserve habitats were used by parrots, and the two dominant habitats—pasture-

lands and coffee plantations—were never used by any species (Table 6). The only artificial habitat used was *Eucalyptus* plantation (by two species). Primary forest was the habitat most preferred for *P. maracana* and *P. maximiliani*, whereas secondary forest was pre-

TABLE 5. Spearman's correlations ( $P < 0.05$  after sequential Bonferroni adjustment;  $n = 70$  plots in all cases) between frequency of flights by parrot groups over 1- × 1-km plots and characteristics of 1- × 1-km plots at Caetetus Reserve, São Paulo state, Brazil (2002).

Habitat/landscape variable	<i>Primolius maracana</i>	<i>Pionus maximiliani</i>	<i>Aratinga leucophthalmus</i>	<i>Brotogeris versicolurus</i>
Pasture	—	+0.36	—	—
Secondary forest	—	—	—	—
Coffee	—	—	—	—
Natural habitats				
Primary forest	-0.31	+0.35	—	—
Riverine forest	—	—	—	+0.27
Scrub	—	—	—	+0.38
Habitat richness	—	—	+0.27	—
Connectivity variables				
Distance to reserve (DIST)	-0.35	-0.58	—	—
Percentage forest between plot and reserve (FOREST)	—	—	—	—
Largest gap in forest between plot and reserve (GAP)	—	—	—	—

ferred by *A. leucophthalmus* and *B. versicolurus*. Riverine habitats were used by all species, but were not used disproportionately to their availability by any species.

## DISCUSSION

Of seven parrot species recorded during our study, only two were regularly encountered in the reserve itself. *B. versicolurus* was recorded flying over and using a variety of habitats in the extra-reserve landscape (particularly those around farms), reflecting its generalist lifestyle (Juniper and Parr 1998). Movements of *A. leucophthalmus* were actually more common well away from the reserve, indicating some avoidance of habitats around the main forest block. Both of these species are

thriving in Brazil's anthropogenic habitats (Juniper and Parr 1998).

The species we were most interested in, *P. maracana*, was frequently recorded both inside and outside the reserve. We could find few specific habitat associations for the species within the reserve, although it did tend to occur in areas of primary forest with few dead trees. Our population estimate for the reserve was 88 birds; however, for two reasons we believe that there are additional populations that spend much or all of their time outside the reserve. First, the within-reserve density estimate was based on data collected during the day at times when some individuals had left the reserve to feed in the surrounding agricultural landscape. Second, we believe that

TABLE 6. Preference index for parrot use of extra-reserve habitats outside Caetetus Reserve, São Paulo state, Brazil (2002). Habitats are ranked according to their use by *Primolius maracana*. Indices are based on the number of birds recorded as perched in the different habitats.

Habitat (%) <sup>a</sup>	Habitat preference index			
	<i>Primolius maracana</i>	<i>Pionus maximiliani</i>	<i>Aratinga leucophthalmus</i>	<i>Brotogeris versicolurus</i>
Primary forest (6.0)	3.8	2.7	0.3	2.3
<i>Eucalyptus</i> (2.1)	2.9	1.0	0	0
Secondary forest (4.5)	2.0	0.7	2.2	12
Riverine (8.0)	0.6	0.3	0.6	0.1
Pasture (42.0)	0	0	0	0
Coffee (33.0)	0	0	0	0
Scrub (2.9)	0	0	0	0
Rubber/orange (1.1)	0	0	0	0

<sup>a</sup> Percent of total extra-reserve habitat.

there is a population of *P. maracana* based well outside the reserve, as a flock of 56 individuals was recorded 9 km south of the reserve. These populations may be large enough for the species to persist in the area, at least in the short term.

Despite being recorded commonly outside the reserve, all four common parrot species were selective as to the extra-reserve habitats they used. The dominant habitats—pasture and coffee plantations—were never used by any species. This is not surprising, as the pasture and coffee crops around Caetetus contained very few remnant or planted trees. Coffee fruits may be used by *P. maracana* at some times of year (e.g., Marsden et al. 2000), but certainly coffee plantations are not attractive or a keystone habitat for any of the parrots. All records of parrot habitat use were in just four habitats, with *Eucalyptus* plantations being the only artificial habitat used. In fact, parrots only selected three habitats more than expected on the basis of their availability in the landscape: secondary forest was selected by three species, primary forest remnants by two species, and *Eucalyptus* plantations by one species.

Studies elsewhere have stressed the importance of dispersal ability and corridors for the use of extra-reserve habitats by animals (e.g., Pires et al. 2002). We calculated three habitat connectivity indices, but only one (DIST) was important in explaining patterns of parrot movements. It may be that the other measures did not reflect barriers to parrot movement, or at least did not add to the explanatory power of using simple distance from the reserve. *P. maracana*—like most, but not all parrots (e.g., Rowley 1983, Marsden et al. 2000)—are regarded as good dispersers, and we suggest that availability of natural forest, rather than mobility, constrains parrot distribution around Caetetus.

Blue-winged Macaws were once found in many states in Brazil, eastern Paraguay, and northeastern Argentina (Juniper and Parr 1998), but the species has become extirpated over much of its range, and further extirpations are predicted in forest fragments (Snyder et al. 2000). Although we do not know what limits the area's populations of parrots, there is general concern about recruitment rates among cavity-nesting parrots (e.g., Mawson

and Long 1994, Snyder et al. 2000), and nest-site availability within the reserve needs to be examined. At a landscape scale, the maintenance of forest remnants around the reserve is most important to the populations of *P. maracana* and other parrots. We suggest that while primary forest may be most preferred by *P. maracana*, other forest types, and even *Eucalyptus*, has some benefit to the parrot assemblage.

Legislation in São Paulo state dictates that 10% of land on private farms be maintained as forest. Our data indicate that for Caetetus, as suggested for other reserves in the Atlantic Forest (Marsden et al. 2000), reforestation in areas adjacent to nature reserves may be disproportionately valuable for enhancing parrot populations, and, presumably, other wildlife that inhabit reserves. The degree of deforestation in the interior of São Paulo is so acute that there is a strong argument for focusing forest-restoration programs almost entirely on landscapes surrounding the region's few reserves.

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## REPRODUCTIVE SUCCESS OF PIPING PLOVERS AT BIG QUILL LAKE, SASKATCHEWAN

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**ABSTRACT.**—Big Quill Lake, Saskatchewan, is an important breeding area for Piping Plovers (*Charadrius melodus*); the area hosts up to 8% of the continental breeding population, yet little is known about how the site contributes to the overall survival of this species. We studied the reproductive success of Piping Plovers at Big Quill Lake from 1993 to 1995. We located 208 nests and captured and banded 456 young. Nest initiation occurred from mid-May to mid-July, and median nest-initiation dates were 14, 13, and 13 May in 1993, 1994, and 1995, respectively. Mean clutch size for presumed first nests was 3.92 eggs. Nesting success was consistently high from 1993 to 1995, with Mayfield estimates of nest success ranging from 75 to 88%; nests initiated later in the season were less successful than earlier nests. The wide beach (200–1,000 m) at Big Quill Lake may have contributed to high nesting success by reducing efficiency of predators. Use of Big Quill Lake beaches by humans and cattle was also minimal. Fledging success varied dramatically, with 0.02, 1.35, and 1.78 young fledged per breeding pair in 1993, 1994, and 1995, respectively. Low productivity of Piping Plovers in 1993 was a result of low chick survival during a week of rain, cold temperatures, and high winds, rather than low nesting success. Fledging success in 1994 and 1995 was higher than the 1.24 chicks per pair required for population stability on alkaline lakes in the Northern Great Plains. This high productivity suggests that Big Quill Lake is an important Piping Plover breeding site and measures should be taken to ensure its continued protection. Received 21 April 2004, accepted 3 March 2005.

Piping Plover (*Charadrius melodus*) numbers have declined continentally in the last 50 years, due in part to permanent destruction of breeding and wintering habitats, and reduced reproductive success (Sidle 1984, Haig 1992). This decline has resulted in the Piping Plover being listed as an endangered species in Canada (Haig 1985), endangered in the Great Lakes region of the United States, and threatened elsewhere in the United States (Sidle 1984). Low reproductive success is considered a limiting factor to the recovery of Piping Plovers in the Northern Great Plains (Haig 1992, Ryan et al. 1993, Murphy et al. 1999); however, this aspect of demography has been documented at relatively few alkali lakes (Haig and Plissner 1992, Plissner and Haig

1997, Murphy et al. 1999). Monitoring reproductive success is considered a priority for the recovery of this species (U.S. Fish and Wildlife Service 1994).

Factors thought to affect reproductive success of Piping Plovers include weather (e.g., Grover and Knopf 1982, Haig and Oring 1988, Sidle et al. 1992), fluctuating water levels (e.g., Mayer 1990, Sidle et al. 1992, Espie et al. 1998, Skeel and Duncan 1998), and egg and chick predation (e.g., Rimmer and Deblinger 1990, Mayer and Ryan 1991, Melvin et al. 1992, Mabee and Estelle 2000). The importance of these factors can vary annually and with the type of breeding site (Larson et al. 2002).

Big Quill Lake, Saskatchewan, is a large alkaline wetland and is an important breeding site for Piping Plovers in North America. In 1996, the site had the largest breeding population (435 birds) of any site in North America—8% of the continental population and 26% of the Canadian prairie population (Skeel et al. 1997). However, numbers fluctuate widely from year-to-year: the last three International Censuses at Big Quill Lake reported 151 adults in 1991 (Haig and Plissner 1992), 435 adults in 1996 (Plissner and Haig 1997), and 105 adults in 2001 (Ferland and Haig 2002); Harris and Lamont (1991) reported 43

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birds in 1989, and Harris estimated over 440 birds in 1995 (W. C. Harris pers. comm. in Skeel et al. 1997).

Even though Big Quill Lake can support a large breeding population of Piping Plovers, there is very little information on Piping Plover reproductive success at this lake and the role it plays in the overall conservation of this species. The purpose of this paper is to examine the reproductive success of Piping Plovers at Big Quill Lake by documenting nesting chronology, nesting success, and fledging success. Knowledge of Piping Plover reproductive success at such an important breeding area will increase our ability to conserve and manage this endangered species.

#### METHODS

*Study area.*—Big Quill Lake (51° 53' N, 104° 15' W) is a large (30,700 ha), shallow, saline basin on the Central Saskatchewan Plains about 200 km east of Saskatoon. The shoreline is primarily alkaline mudflats, and is approximately 200 km long when the basin is full. The upper beaches are partially to fully vegetated with alkali grass (*Distichlis stricta*), western sea-blite (*Suaeda depressa*), Nuttall's salt-meadow grass (*Puccinellia nuttalliana*), northern reed grass (*Calamagrostis inexpectata*), and wild barley (*Hordeum jubatum*). In 1993 and 1994, the basin was approximately 60% flooded, and beach width was approximately 1,000 m (Harris 1993, 1994). In 1995, the water level in Big Quill increased due to heavy snowfall the previous winter, resulting in a beach width of <200 m (Harris 1995).

*Nest surveys.*—Our study area was located on the east side of Big Quill Lake and composed approximately one-third of the shoreline. During 1993–1995, we surveyed the study area at least twice weekly from 7 May to 30 August. We searched for territorial pairs of Piping Plovers (birds calling, exhibiting aggressive or defensive behavior, or performing courtship displays) by systematically walking or slowly traversing the shoreline with an all-terrain vehicle (ATV). We watched territorial birds from a distance of 50–100 m, which allowed birds to return to their nest. We plotted the location of all birds on a map of the study area. We marked nests with pin-flags placed at least 30 m away in the adjacent vegetation, and plotted nest locations on an aerial photo-

graph of the shore. We determined nest occupancy using a 15–60× telescope from a distance of 50–100 m during repeat visits. We visited nests every 3 days during initiation and early incubation. Most nests were located during egg-laying; when full clutches were found, a single egg was floated to estimate incubation stage (Schwalbach 1988). We estimated hatch dates assuming a 6-day egg-laying period and a 28-day incubation period (Whyte 1985). We used this information to return to nests near hatching and band chicks before they moved away from their nest. Although young plovers generally left the nest scrape shortly after the last egg hatched, they were rarely far from the scrape during the first few days, and the broods remained close to their nest site until they were capable of flight.

Chicks were banded with a standard federal aluminum leg band, and either one or two colored celluloid bands to allow for further recognition without recapture. Color-banded broods were checked every 2 to 3 days to monitor survival and movements, and all nests and broods were followed until fledging or nest failure. Young that disappeared after they reached 21 days of age were considered to have fledged (Haig 1992). We defined fledging rate as the number of young fledged per breeding pair. Murphy et al. (1999) suggest that fledging rate is the most important measure of reproductive success for the Piping Plover, because it represents “a direct link to recruitment.” We defined the number of breeding pairs as the number of first nests. We distinguished first nests from late nests based on break points in nest-initiation dates, and assumed that late nests were renests. Between mid-July and mid-August, we made weekly visits to six staging areas located outside the study area to check for marked young that may have been alive but missed during surveys of the study area.

*Statistical analysis.*—We used the Mayfield method to estimate nesting success (Mayfield 1961, 1975). Nests were considered successful if at least one chick hatched. Mayfield nest success was defined as  $(1 - \text{daily mortality rate})^N$ , where daily mortality rate = number of nest losses/total exposure days, and N = nesting period. The average nesting period from nest initiation (first egg) to hatching (first hatch) was 33 days. We also estimated egg

TABLE 1. Nesting chronology, clutch size, and reproductive success of Piping Plovers at Big Quill Lake, Saskatchewan, 1993–1995.

Productivity variable	1993	1994	1995
Median nest-initiation date (range)	14 May (10 May–11 July)	13 May (10 May–21 June)	13 May (10 May–21 June)
Number of nests	51	73	84
Number of first nests <sup>a</sup> (and presumed renests)	42 (9)	71 (2)	83 (1)
Number of eggs laid (mean ± SE)	183 (3.59 ± 0.12)	280 (3.84 ± 0.06)	333 (3.96 ± 0.00)
Number of chicks hatched (mean ± SE)	144 (2.82 ± 0.24)	231 (3.16 ± 0.18)	287 (3.42 ± 0.15)
Number of chicks fledged (mean ± SE)	1 (0.02 ± 0.02)	96 (1.32 ± 0.17)	148 (1.76 ± 0.16)
Daily survival rate of nests (DSR) <sup>b</sup>	0.991	0.994	0.996
Mayfield nest success (95% CI) <sup>c</sup>	0.752 (0.63–0.89)	0.822 (0.73–0.92)	0.875 (0.80–0.95)

<sup>a</sup> First nests were distinguished from renests based on a break point in nest-initiation dates. Nests initiated after 27 June, 20 June, and 20 June for 1993, 1994, and 1995, respectively, were considered renests.

<sup>b</sup> Daily Survival Rate (DSR) = (1 - number of losses/total exposure days).

<sup>c</sup> Mayfield nest success =  $DSR^{33}$  (33 is the calculated average nesting period from nest initiation [first egg] to hatching); SE =  $\{[DSR(1 - DSR)]/total\ exposure\ days\}^{32}$ ; 95% Confidence Limits =  $[DSR \pm 2(SE)]^{33}$ .

success (proportion of eggs that hatched) and fledging success (mean number of fledglings per breeding pair).

We used Cox regression survival analysis to examine the effect of year on survival of broods. The Cox proportional hazards model (Cox 1972) models the hazard rate or the rate of failure. The hazard rate is assumed to be a function of time, but this method does not attempt to characterize the function (Nur et al. 2004). The null hypothesis is that the ratio of hazard rates = 1 (i.e., no difference between groups). Survival analysis includes time-to-death and time-to-end-of-monitoring data for broods that were still alive when monitoring ceased. Survival analysis is useful when the ultimate outcome may be uncertain (i.e., when it is not possible to continue monitoring nests due either to weather or the culmination of the nesting cycle). For our study, we were certain how long broods survived, but only until monitoring ceased. Data are considered to be right-censored when the start time is known, but (brood) failure time is unknown. Our data were right-censored because there was incomplete information on the outcome (i.e., we do not know when all individuals died). We defined survival time as time from hatch to the last day chicks were observed. Chicks were assumed to have died if they disappeared be-

fore 21 days of age. As long as one chick in each brood survived to the end of monitoring, the brood was still considered to be alive. We compared brood survival for 1993 to 1995 and 1994 to 1995.

We used the Kruskal-Wallis rank sum test to determine whether nest-initiation data varied among years, and we used linear regression to determine whether clutch size decreased with nest initiation. We used logistic regression to determine whether nest and fledging success—both measured as binary response variables (1 = success, 0 = failure)—were dependent on nest-initiation date (all nests combined). We used S-PLUS (Mathsoft, Inc. 1997) to conduct statistical analyses. Means are presented ± SE.

## RESULTS

*Nest chronology.*—We found 208 nests and captured and banded 456 young on the east side of the lake (Table 1). We banded 140 of 148 hatched young in 1993, 129 of 232 in 1994, and 187 of 288 in 1995.

Egg-laying commenced by the 2nd week in May and continued until the 2nd week in July. Over half of all nests were initiated in a 4-day period from 11 to 14 May. The median date of nest initiation was 14, 13, and 13 May in 1993, 1994, and 1995, respectively, and did

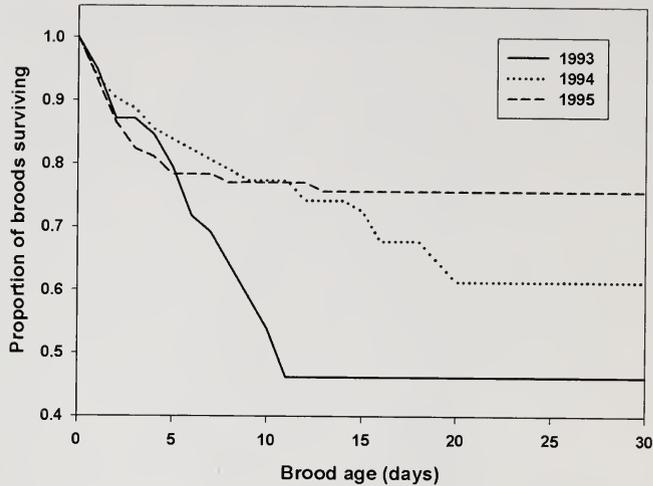


FIG. 1. Proportion of Piping Plover broods surviving (presumed) from hatching to fledging at Big Quill Lake, Saskatchewan, 1993–1995. Chicks that disappeared after 21 days were assumed to have fledged.

not differ among years (Kruskal-Wallis  $\chi^2 = 0.52$ ,  $df = 2$ ,  $P = 0.77$ ,  $n = 208$ ). However, in 1993, 18% ( $n = 9$ ) of nests were initiated after 26 June, whereas in 1994 and 1995, no nests were initiated after this date.

We estimated 42, 71, and 83 breeding pairs in 1993, 1994, and 1995, respectively, based on the estimated number of first nests. In 1993, no nests were initiated between 2 and 26 June; thus, we assumed that the nine nests initiated after 26 June were renests. In 1994, no nests were initiated between 14 and 20 June and the two nests initiated after 20 June were considered renests. In 1995, no nests were initiated between 14 and 20 June and we assumed that the single nest initiated on 21 June was a renest.

**Clutch size.**—Mean clutch size was  $3.92 \pm 0.02$  eggs/clutch for presumed first nests and  $2.25 \pm 0.28$  eggs/clutch for late nests (all years combined). Clutch size decreased with nest-initiation date (linear regression:  $\beta = -0.035$ ,  $SE = 0.002$ ,  $F_{1,207} = 461.27$ ,  $P < 0.001$ ). Late nests had a mean of  $1.89 \pm 0.2$  ( $n = 9$ ),  $3 \pm 1$  ( $n = 2$ ), and  $4$  ( $n = 1$ ) eggs per nest in 1993, 1994, and 1995, respectively. Of 51 nests initiated in 1993, 2% ( $n = 1$ ) had five eggs, 75% ( $n = 38$ ) had four eggs, 8% ( $n = 4$ ) had three eggs, 12% ( $n = 6$ ) had two eggs, and 4% ( $n = 2$ ) had one egg. In 1994, of 73 nests initiated, 88% ( $n = 64$ ) had four eggs, 8% ( $n = 6$ ) had three eggs, and 4% ( $n = 3$ ) had two eggs. Of 84 nests initiated in

1995, 1% ( $n = 1$ ) had five eggs, 94% ( $n = 79$ ) had four eggs, and 5% ( $n = 4$ ) had three eggs.

**Nesting success, fledging success, and brood survival.**—Mayfield nest success was high in all years (75, 82, and 88% in 1993, 1994, and 1995, respectively). The probability of nesting success decreased with later nest-initiation dates (logistic regression:  $\beta = -0.040$ ,  $SE = 0.012$ ,  $t = -3.50$ ,  $df = 1$ ,  $P < 0.001$ ). One percent ( $n = 1$ ), 42% ( $n = 96$ ), and 52% ( $n = 148$ ) of chicks fledged in 1993, 1994, and 1995, respectively. In 1993, 0.02 young fledged per breeding pair, whereas in 1994 and 1995 fledging success was 1.35 and 1.78 per pair. Nests with later hatch dates had lower fledging success (logistic regression:  $\beta = -0.047$ ,  $SE = 0.017$ ,  $t = -2.85$ ,  $df = 1$ ,  $P = 0.001$ ). Brood survival was lower in 1993 than in 1995 ( $Z = 3.45$ ,  $P < 0.001$ ), but was not significantly different between 1994 and 1995 ( $Z = 1.73$ ,  $P = 0.084$ ; Fig. 1).

## DISCUSSION

Median nest-initiation dates in this study were similar to those found at Big Quill Lake in 1980 and 1981 (13 May and 9 May; Whyte 1985), and at Lake Diefenbaker, Saskatchewan (e.g., 12 May in 1992 and 9 May 1993; Espie et al. 1998). However, the 1993 nesting attempts at Big Quill Lake were the latest reported in over 10 years of monitoring, and no young fledged from those nests (Harris 1993).

Harris (1993) attributed the late nesting to large losses of nests and broods in early spring during a period of inclement weather. Piping Plovers can renest once or twice in a season if the eggs are destroyed, and there are records of them producing two broods in a year (Bottitta et al. 1997); however, usually they raise only one brood per year (Haig 1992).

A seasonal decline in clutch size and reproductive success has been well documented for birds in general (e.g., Lack 1968, Klomp 1970, Perrins 1970, Daan et al. 1989), and Piping Plovers in particular (Knetter et al. 2002). We found a similar pattern of larger clutch sizes and greater hatching success in early nests. We also found that clutch sizes of Piping Plovers at Big Quill Lake were similar to those reported from other studies (Haig 1992). The smaller average clutch sizes in 1993 were likely the result of a large renesting effort. Declines in reproductive success over a season are thought to be related to physiological or energy demands related to timing of breeding (Lepage et al. 1999), or to lower quality or fitness of later breeders (Verhulst et al. 1995).

Mayfield nest success was consistently high from 1993 to 1995 and was greater than nest success estimates from other sites (e.g., Mayer and Ryan 1991, Patterson et al. 1991, Loegering and Fraser 1995, Mabee and Estelle 2000, Lauro and Tanacredi 2002). Several factors may explain the high nest success at Big Quill Lake from 1993 to 1995. First, predation pressure at Big Quill Lake may be lower than at other lakes in the region due to the relatively wide shoreline, which lowers the probability of predators detecting nests (Prindiville Gaines and Ryan 1988, Espie et al. 1996). Even though we observed a dramatic change in the average distance from nesting sites to water from 1994 to 1995, productivity changed little between these years, suggesting that beach width in 1995 (200 m) was still above the minimum threshold required for good nesting success. In fact, productivity was slightly higher in 1995, when the beach was narrower, suggesting that even when water levels are high at this lake, the distance from water to nesting sites, and/or from permanent vegetation to nest sites, may still be sufficient to allow for high nest and fledging success. In addition to the wide beach, there are few trees,

shrubs, or other perch sites in proximity to the nesting areas around Big Quill Lake, which may have reduced perching opportunities for avian predators. Disturbance by humans and cattle was low at Big Quill Lake, but is known to reduce productivity in some areas (e.g., Burger 1994). Mayfield nest success estimates from our study, and from more recent studies at Big Quill Lake (2002–2004; C. Gratto-Trevor unpubl. data), also were greater than those recorded at Big Quill Lake in the early 1980s (16% and 29%, Whyte 1985); the reason for this difference is unknown.

Although Piping Plover nest success was high from 1993 to 1995, fledging success varied among years, which is typical of this species (Haig and Oring 1987, Maxson and Haws 2000, Knetter et al. 2002). At alkaline lakes in the Great Plains, Piping Plover reproductive success averages 0.89 fledglings per pair without predator exclusion, and 1.28–1.78 fledglings per pair with predator exclusion (Larson et al. 2002). Larson et al. (2002) determined that a mean reproductive success of 1.24 fledglings per pair would be required at alkaline lakes to stabilize a declining population of Piping Plovers. This target was exceeded in 1994 and 1995 at Big Quill Lake, and it was greater than Whyte's (1985) 0.76 fledglings per pair at Big Quill Lake a decade earlier (although the low reproductive success reported by Whyte [1985] was due, in large part, to a lower rate of nesting success as opposed to fledging success). The high reproductive success at Big Quill Lake during 1994 and 1995 suggests that—at least in some years—this area may serve as a source for Piping Plovers in the Northern Great Plains.

Low fledging success in 1993 may be due, in part, to a period of prolonged heavy rainfall, combined with cold temperatures and high winds (Harris 1993). Prior to 27 June, 55% of young were still alive, after which there was a long period of inclement weather. Once conditions had improved sufficiently to allow monitoring to resume on 7 July, all young and eggs had disappeared from the study area and a renesting effort was under way. The only chick that was known to have fledged in 1993 was later found at a staging area. It is probable, however, that other young fledged during this period of no monitoring, and were not accounted for at staging areas

later in the season. Seventeen broods were 13–15 days old before monitoring temporarily ceased and some of these chicks may have fledged before monitoring resumed 9 days later. We feel that the low number of birds fledging in 1993 is likely an underestimate, although similarly low numbers of young Piping Plovers observed at the Big Quill Lake staging areas corroborates low fledging success in 1993. Survival analysis also suggests that brood survival was lower in 1993 than 1995, but was not different between 1994 and 1995, corroborating the low fledging success in 1993.

Our study suggests that Big Quill Lake may serve as a population source for Piping Plovers in the Great Plains. The low productivity of Piping Plovers at Big Quill Lake in some years may be a result of low chick survival rather than low nesting success. Because of the numbers of nesting pairs and recent high productivity, the importance of Big Quill Lake as a breeding area for Piping Plovers is evident. Measures should continue to ensure its protection and integrity.

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## BREEDING ECOLOGY OF WHITE-WINGED DOVES IN A RECENTLY COLONIZED URBAN ENVIRONMENT

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**ABSTRACT.**—Using field-implanted subcutaneous radio transmitters, we monitored the breeding biology of White-winged Doves (*Zenaida asiatica*) in a recently colonized urban area (Waco, Texas). We implanted transmitters in June 2002 ( $n = 39$ ; 16 males, 23 females) and February and March 2003 ( $n = 40$ ; 17 males, 17 females, 6 unknown sex), and tracked radio-tagged doves every 3rd day until transmitters no longer functioned (90–120 days). We tracked 26 doves to 36 nests in nine tree species. The maximum number of nesting attempts was four. Nest success of first and second nesting attempts was 62 and 24%, respectively, and overall nest success for both years combined was 52%. Mean nest height—as a proportion of tree height—ranged from 0.31 to 0.75. Urban White-winged Doves had an extended breeding season; nesting attempts occurred both before and after the traditional dove breeding period in native brush habitats of the lower Rio Grande Valley of Texas. Field-implantation of subcutaneous radio transmitters was a viable technique for monitoring nesting activities of White-winged Doves. Received 20 August 2004, accepted 13 March 2005.

Over the last 40 years, the distribution of White-winged Doves (*Zenaida asiatica*) has undergone substantial change (Schwertner et al. 2002). Until the mid-1970s, the breeding range in Texas was limited mainly to four counties (Cameron, Starr, Hidalgo, and Willy) in the lower Rio Grande Valley (LRGV) at the extreme southern tip of the state (Cottam and Trefethen 1968, George et al. 1994). Since then, White-winged Doves have been expanding their range northward; the species has been recorded in Canada (Rogers 1998), with breeding documented as far north as Kansas (Moore 2001). The majority of breeding individuals in the United States, both currently and historically, resides in Texas (George et al. 1994).

White-winged Dove populations have increased substantially over the past 20 years, but only 16% of the Texas population now occurs in the LRGV (G. L. Waggener pers. comm.). Large breeding populations of White-winged Doves have become established in central Texas, with numerous smaller, satellite populations occurring throughout the state. Concurrent with the northward range expansion, White-winged Dove populations are now concentrated in urban areas (West et al. 1993).

This represents a dramatic shift in habitat use away from thorn scrub and riparian woodlands of the Tamualipan biotic province (Blair 1950) that characterizes the LRGV (West et al. 1993, Schwertner et al. 2002).

Loss of native habitat and extensive agricultural and industrial development in the LRGV have influenced the distribution of White-winged Doves in Texas (Hayslette et al. 1996). From 1900 to 1950, about 95% of the historic, native breeding habitat was converted for human uses, resulting in significant loss of old-growth woodlands and water diversions from the Rio Grande and Arroyo Colorado (Kiel and Harris 1956, Cottam and Trefethen 1968). In addition, severe freezes occurring in 1951, 1962, 1983, and 1989 decimated citrus groves that White-winged Doves had used increasingly as nesting sites, most likely in response to loss of native habitat (Cottam and Trefethen 1968, George et al. 1994).

A substantial proportion of White-winged Doves concentrating in urban areas north of the LRGV are non-migratory (George 1991, West et al. 1993, Hayslette and Hayslette 1999). Anecdotal evidence suggests that an extended breeding season by non-migratory doves could lead to increased recruitment, with individuals producing clutches before and after the traditional nesting period (Hayslette and Hayslette 1999).

The objective of our study was to document habitat use and productivity of White-winged Doves breeding in a recently colonized urban

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environment. To track doves, we used subcutaneously implanted radio transmitters. This is the first radiotelemetry-based study of White-winged Dove breeding ecology in a metropolitan area.

## METHODS

We conducted our study in Waco, Texas (McLennan County), because of its northern location and relatively recent colonization by White-winged Doves; dove densities are high and the human population (202,983; U.S. Census Bureau 2000) provides potential sources of food, water, and habitat. White-winged Doves were first recorded in Waco on the Audubon Christmas Bird Count in 1990, and they were first observed breeding there in 1993. In 1999, 2001, 2002, and 2003, Texas Parks and Wildlife Department personnel conducted call-count surveys of White-winged Doves in Waco, subsequently deriving a population estimate of approximately 70,000 doves.

Our study area boundary was the city limits of Waco. White-winged Doves preferentially congregated in older (>30 years) neighborhoods with relatively high densities of mature ornamental trees. The dominant tree species, which accounted for the majority of the canopy, were oaks (*Quercus* spp.) and pecan (*Carya illinoensis*). We also observed that, with the exception of fall feeding flights to areas outside of Waco, doves obtained food and water locally, primarily from anthropogenic sources.

We trapped White-winged Doves using standard walk-in wire funnel traps (Reeves et al. 1968) baited with a 2:1 mixture of chicken scratch and black-oil sunflower seeds (Purina Corp., St. Louis, Missouri). In June 2002, we surgically implanted subcutaneous transmitters in 39 White-winged Doves (16 males, 23 females), and, in February and March 2003, we implanted transmitters in another 40 doves (17 males, 17 females, 6 unknown sex). We monitored doves from 10 July to 4 September in 2002 and from 31 March to 18 June in 2003. Gender was determined using an infant nasal speculum to examine the cloaca and identify conical papillae in males or an oviduct opening in females (Miller and Wagner 1955, Swanson and Rappole 1992). We performed transmitter implants in the field using

a portable anesthesia machine and mobile surgical lab (Small et al. 2004). Implanted individuals were released after they had completely regained a coherent state with no signs of impairment. Transmitters (Advanced Telemetry Systems, Isanti, Minnesota) weighed 3.7 g (approximately 2.0% of body weight) and were  $25 \times 14 \times 7$  mm with an external, 16-cm-long whip antenna. All research was conducted in accordance with the Texas State University Institutional Animal Care and Use Committee, approval number 5QEKCT02.

Using a vehicle-mounted, omni-directional antenna and a handheld, four-element, directional yagi antenna (White and Garrott 1990), we tracked radio-tagged doves for the duration of transmitter function (50–80 days). We documented nesting (time, date, location, and status) and habitat (tree species, nest height, and tree height) parameters. We monitored active nests every 3rd day using binoculars, and, when feasible, an extendable fiberglass pole with a mirror (Parker 1972). We calculated nest success rates using Mayfield methods (Mayfield 1961, 1975). For reasons discussed in Johnson (1979), we did not use the Mayfield-40% method (Miller and Johnson 1978) or the maximum-likelihood method. The Mayfield-40% method might have proven more appropriate if the mean nest-visitation rate was  $\geq 15$  days; the maximum-likelihood method is subject to bias unless sample sizes are large (Miller and Johnson 1978). We calculated standard errors and 95% confidence intervals for nesting success following Johnson (1979).

Both male and female White-winged Doves participate in nest building, incubation, and brooding; nests are constantly attended by at least one adult (Schwertner et al. 2002). Because of constant nest attendance, we assumed equal probability of egg and nestling survival. Because White-winged Doves in urban areas do not reuse nests (White-winged Doves produce multiple clutches; Gray 2002, Schaefer 2004), there was no bias due to age heterogeneity of nests. We were unable to establish hatching dates because most nests were too high.

We considered a nest active if it was attended by an adult, and we considered it successful if at least one young fledged from the nest. Time to fledging was based on a 14-day

TABLE 1. Mayfield nest success (standard error) and 95% confidence intervals, by nest attempt and year, Waco, Texas, 2002–2003.

Nest attempt/year	No. exposure days	No. nests	No. nests failed	Nest success (SE)	95% CI
1st/2002	245	13	3	0.708 (0.007)	0.701–0.715
1st/2003	217	12	5	0.521 (0.010)	0.510–0.531
All/2002	264	14	4	0.652 (0.008)	0.644–0.660
All/2003	296	20	9	0.421 (0.010)	0.411–0.431
1st/2002, 2003	462	25	8	0.613 (0.006)	0.607–0.619
2nd/2002, 2003	70	6	3	0.293 (0.024)	0.269–0.318
All/2002, 2003	560	34	13	0.518 (0.006)	0.517–0.524

incubation period and a 14-day brooding period (Cottam and Trefethen 1968, Schwertner et al. 2002). Nest success was calculated as  $(1 - [\text{number of nests failed}/\text{number of nest exposure days}])^{28}$ . The exponent of 28 represents combined egg and nestling exposure periods of 14 days each (Schwertner et al. 2002). Standard errors were calculated as the square root of  $1/([\text{number of nest exposure days}]^3/[\text{number of nest exposure days} - \text{number of failed nests}][\text{number of failed nests}])$ .

We tested for differences in nest success between years for first nesting attempts and for all attempts combined, and we tested for differences between first and second nesting attempts for both years combined. Nest success was considered significantly different if there was no overlap in 95% confidence intervals (Sokal and Rohlf 1995). Nest success for third and fourth nesting attempts was not calculated separately because of small sample size ( $n = 2$ ). One first nest attempt in 2002 was excluded from analysis because young fledged on the day we located the nest.

## RESULTS

From 10 July to 4 September 2002, we tracked 14 of the 39 radio-tagged White-winged Doves (8 males, 6 females) to 15 nests. From 31 March to 18 June 2003, we tracked 12 of the 40 radio-tagged doves (7 males, 3 females, 2 unknown sex) to 20 nests, including 1 pair in which both individuals were radio-tagged. In 2002, seven males and six females nested once and one male nested twice. In 2003, five males and two females nested once, two males and one bird of unknown gender nested twice, one bird of unknown gender nested three times, and one female nested four times.

We located the 35 nests in nine tree species, primarily in pecan (48.5%) and sugarberry (*Celtis laevigata*; 17%). The remaining 34.5% occurred in live oak (*Quercus virginiana*), cedar elm (*Ulmus crassifolia*), chinaberry (*Melia azedarach*), crapemyrtle (*Lagerstroemia indica*), pomegranate (*Punica granatum*), Texas oak (*Q. buckleyi*), and glossy privet (*Ligustrum lucidum*). Mean nest height, as a proportion of tree height, was 0.55 in pecan, 0.41 in sugarberry, and 0.45 in the other seven tree species.

Nest success was 0.652 in 2002, 0.421 in 2003, and 0.518 for both years combined (Table 1). Nest success for first nesting attempts and for all nesting attempts combined was significantly lower in 2003 than in 2002. Nest success for second nesting attempts was significantly lower than for first nesting attempts (both years combined). Nest success for all nests for both years was 0.518 (SE = 0.006; Table 1).

## DISCUSSION

White-winged Doves in Waco, Texas, have an extended breeding season. Historically, May to mid-August has been the period of greatest White-winged Dove breeding activity, particularly in the LRGV (Cottam and Trefethen 1968, George et al. 1994, Schwertner et al. 2002). However, in five newly colonized urban populations in Texas, hatching-year White-winged Doves have been observed every month of the year (MFS pers. obs.).

Twenty-three percent of radio-marked White-winged Doves attempted more than one nesting, compared with 39% reported for Kingsville, Texas (Gray 2002). In 2003, one of our radio-marked females nested four times, the first and fourth attempts having

been successful (Schaefer et al. 2004). Cottam and Trefethen (1968) also report multiple nestings during the breeding season; others list the mean as two broods per season (Schwertner et al. 2002).

Overall nest success was 51.8% compared with 58% (Hayslette and Hayslette 1999) and 53% (Gray 2002) in Kingsville, Texas, and 39 to 73% for San Antonio, Texas (West et al. 1993). Earlier monitoring of nests in 2003, prior to the historic peak-breeding time of July (Cottam and Trefethen 1968, Schwertner et al. 2002), may have been the reason for the significant difference in nesting success between years in Waco. When we first began monitoring in 2003, nest trees had not reached maximum foliage development, which resulted in less protective cover and possibly in increased nest failure from exposure to adverse weather and potential predators.

The majority of nests were located in deciduous trees. Nest-tree species were similar in growth form to woodland riparian species native to areas traditionally used by nesting White-winged Doves in the LRGV (Cottam and Trefethen 1968, Schwertner et al. 2002) and Kingsville, Texas (Gray 2002). In urban areas, shade trees such as pecan, live oak, and hackberry are important species for nesting for White-winged Doves (Nilsson 1943, Cottam and Trefethen 1968, West et al. 1993). Although they now nest outside the LRGV—possibly due, in part, to habitat loss (Purdy and Tomlinson 1991)—White-winged Doves seem to select nest trees with growth forms and habits similar to those of the LRGV (Hayslette et al. 1996). The nest heights that we observed—the middle one-third of the tree—were consistent with those recorded in other studies (Small et al. 1989, Gray 2002). Trees less than 3-m high were rarely used for nesting.

**Conclusions.**—Fragmentation of habitat in the LRGV, primarily due to converting native habitat for agriculture (Purdy and Tomlinson 1991, Brush and Cantu 1998), has resulted in the loss of more than 95% of traditional White-winged Dove breeding habitat in Texas. In addition, changes in water-management practices, increased urbanization, and industrialization have degraded breeding habitat for White-winged Doves (Curtis and Ripley 1975).

The distribution of White-winged Doves in Texas has undergone substantial change over the past 50 years, with the most dramatic changes beginning about 1970 (Schwertner et al. 2002). The primary change in White-winged Dove ecology has been the establishment of numerous new populations resulting from a northward range expansion and concurrent colonizing of urban areas by breeding populations (Small et al. 1989, West et al. 1993). To our knowledge, an increase in breeding range combined with such a dynamic change in fundamental, ontogenetically based behavior are unprecedented in bird species native to the New World. The only other analogous scenario has been the range expansion of the Eurasian Collared-Dove (*Streptopelia decaocto*); in about 1900, the species began a similar expansion of its breeding range northward across Europe from its core population in northern India. Breeding populations now are established as far north as Scandinavia (Hollom et al. 1988, Jonsson 1992, Ehrlich et al. 1994).

The change in the distribution of White-winged Doves has revealed large gaps in our understanding of its natural history and ecology, particularly in recently established populations. Year-round residency, nesting in urban environments, and breeding in every month of the year (Hayslette and Hayslette 1999) are drastic departures from dove behavior exhibited prior to 1950, when the species was primarily restricted to the LRGV of Texas (Cottam and Trefethen 1968, George et al. 1994).

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## SPOTLIGHT SURVEYS FOR GRASSLAND OWLS ON SAN CLEMENTE ISLAND, CALIFORNIA

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**ABSTRACT.**—According to Breeding Bird Survey data, grassland birds are among the most imperiled species in North America. Within this group, grassland owls show steep population declines across the United States. Despite these declines, questions still remain regarding the seasonal and geographic distribution of grassland owls. On San Clemente Island (SCI), California, grassland owls are known to occur, but nothing is known about their distribution or abundance. To increase our understanding of owl populations on SCI, we used night-time spotlighting to survey for grassland owls from October 2001 to October 2002. We recorded 733 detections of three species of owls: Barn Owl (*Tyto alba*), Burrowing Owl (*Athene cunicularia*), and Short-eared Owl (*Asio flammeus*). Barn ( $8.3 \pm 0.8$  owls/hr) and Burrowing owls ( $2.2 \pm 0.7$  owls/hr) were the most frequently detected species, whereas Short-eared Owls were rarely detected ( $0.2 \pm 0.1$  owls/hr). We detected owls during all night-time hours surveyed and detected Barn Owls in every month of the study. We detected Burrowing Owls only from October to March and Short-eared Owls from December to April, suggesting that they are winter visitors. Despite the bias of increased detectability using roadside surveys, spotlighting from a vehicle enabled us to efficiently cover a large proportion of the island (compared to walking surveys) and survey multiple grassland species using one survey technique. Received 8 August 2003, accepted 22 February 2005.

Grassland birds are among the most imperiled wildlife in North America (Peterjohn and Sauer 1999, Sauer et al. 2004), and, within this group, owls are considered species of conservation concern in most North American regions (Wellicome and Haug 1995, Herkert et al. 1996, Sheffield 1997, U.S. Fish and Wildlife Service 2002). Biologists visiting and working on San Clemente Island (SCI), California, have observed Barn (*Tyto alba*), Burrowing (*Athene cunicularia*), and Short-eared (*Asio flammeus*) owls at various times of the year and have documented breeding by Barn Owls (BLS and ELK unpubl. data). However, little else is known about the owl populations on SCI.

Grasslands compose 30% (~4,300 ha) of SCI's vegetation community; thus, there is ample habitat for grassland owls. The presence of large, open grasslands on SCI has resulted from the island's history of ranching and the introduction of feral grazers and exotic grasses in the mid-1800s (Andrew 1998). These introductions dramatically altered the

landscape by changing the shrub component of the native coastal chaparral habitats to open grasslands (Coblentz 1980; BLS and ELK unpubl. data). In 1993, however, feral grazers were removed from SCI; as a result, successional change has been allowed to take place and the grasslands are reverting to more natural, shrubby communities.

Due to successional change, the conservation status of the island's owls, and our lack of knowledge about grassland owls on SCI, we examined the presence/absence, relative abundance, and distribution of grassland owls on SCI. We hope to provide a better understanding of how grassland owls use SCI and determine how the successional transition of grassland habitats may effect these owl populations in the future.

### METHODS

*Study area.*—SCI (32° 50' N, 118° 30' W) is located approximately 109 km northwest of San Diego, California, and is the southernmost California Channel Island. The 14,603-ha island is 34 km long and 2.4–6.4 km wide. A relatively level, open plateau runs the length of the island, with elevations ranging from sea level to 599 m. Deep canyons of varying lengths incise the plateau from the east and west sides. Temperatures range from 6 to 37° C and mean annual precipitation is 17.8 cm (California State Northridge, Depart-

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ment of Geography unpubl. data, 1998–2002). Fog is common, especially in the summer. Prevailing winds are from the west, and windy days are frequent throughout the year (typically Beaufort scores of 2–3). SCI is administered by the U.S. Navy and is used for active military training as part of the Southern California Offshore Range; however, the U.S. Navy has an environmental program to protect natural and cultural resources (U.S. Department of the Navy 2001).

Suitable owl habitat (i.e., grasslands and maritime desert scrub) is found predominantly on, and surrounding, the island's large central plateau. Grasslands comprise native and non-native species (*Avena* spp., *Bromus* spp., *Nassella pulchra*) and scattered shrubs such as coyote brush (*Baccharis pilularis*); however, after the removal of feral grazers in 1993, shrub cover has increased (J. Dunn pers. comm.). Maritime desert scrub is dominated by boxthorn (*Lycium californicum*), snake cactus (*Bergerocactus emoryi*), cholla (*Opuntia prolifera*), prickly pear cactus (*Opuntia littoralis*), California sagebrush (*Artemisia californica*), and morning glory (*Calystegia macrostegia*). See Raven (1963) and Kellogg and Kellogg (1994) for a more detailed description of SCI's vegetation.

*Survey technique.*—Because of the inaccessible nature (i.e., steep, rocky canyons) of potential nesting habitat for some owl species and the limited availability of personnel to search the vast grassland expanses, we surveyed for owls along established island roads. We established eight 10-km transects (Fig. 1). We selected transect starting points randomly while ensuring that no two transects overlapped. Although SCI roads were not established randomly and roadside surveys are associated with certain biases (Bart et al. 1995, Keller and Scallan 1999), the layout of the island road system offered access to most of the open grassland and maritime desert scrub habitat; the view from the roads was typically unobstructed on either side. Our survey transects sampled approximately 55% (77.5 km) of the available roads on SCI, and provided a representative sample of owl habitat across the island (i.e., they traversed ~34% of the grassland on the island).

We surveyed each transect once per month over a 13-month period (October 2001 to Oc-

tober 2002) for a total of 104 surveys (13 all-island surveys). We tried to survey as many of the eight transects in one night as possible, and each month we randomized the order in which we surveyed the eight transects. We conducted surveys by driving transects in a truck at night and using spotlights to locate owls (hereafter spotlighting). The driver and passenger, equipped with 750,000-candle power spotlights, scanned both sides of the road, making full sweeps of the plateau and road ahead while driving 16–32 km/hr (depending on road conditions). We used binoculars (7 × 42 and 8 × 42) to identify species and plotted the locations of flying or perched birds on a topographic map. We recorded the time of detection, species, and behavior at detection (e.g., perched, hunting, flushed) for each individual located.

Some transects (e.g., R3, R4, and R5) included multiple dead-end spur roads; in these situations we backtracked over the same road in order to resume the survey, only recording observations while traveling in the initial direction along the spur. From March to October 2002, one transect (R2) was shortened to 6 km due to a change in the accessibility to that part of SCI. We surveyed the shortened route for those 8 months, and adjusted the total distance surveyed to 76 km, rather than 80 km.

Under optimal weather conditions (e.g., clear skies, no fog), the maximum distance at which we could reliably detect owls was approximately 250 m (determined using a Barn Owl replica, spotlight, and digital rangefinder). We did not conduct surveys in fog or rain, or when wind exceeded a score of 6 on the Beaufort scale (~40–50 km/hr). Temperatures between 12 and 14°C, cloud cover between 0 and 25%, and wind speed of 2 or 3 on the Beaufort scale (~8–19 km/hr) were typical survey conditions.

Because SCI is an active training facility for the U.S. Navy, designing a straightforward survey design was challenging. We had to adjust our methodology to account for geographic and temporal (both seasonal and hourly) access restrictions, usually on short-notice. On some nights we were denied access to certain areas of the island. When we were unable to survey all transects in one night, we finished the surveys on the next available date when access was granted. These restrictions created



FIG. 1. Map of eight roadside transects used to survey grassland owls on San Clemente Island, California, 2001 and 2002.

uneven survey coverage; no surveys were conducted during some time-blocks (i.e., 10, 11, and 12 hr past sunset) and, during others, we were given regular access. These access constraints prevented us from standardizing how transects were surveyed over various time-blocks, which could influence survey results if there are time-dependent associations in owl activity. However, because we had little

control over when each transect could be surveyed, these constraints simply aided the randomization of our design.

*Data analysis.*—To determine patterns of temporal and seasonal activity, we (1) summed the amount of time surveyed in each hour after sunset for each month of the study, (2) totaled the number of owl detections within each 1-hr time block, and (3) calculated the

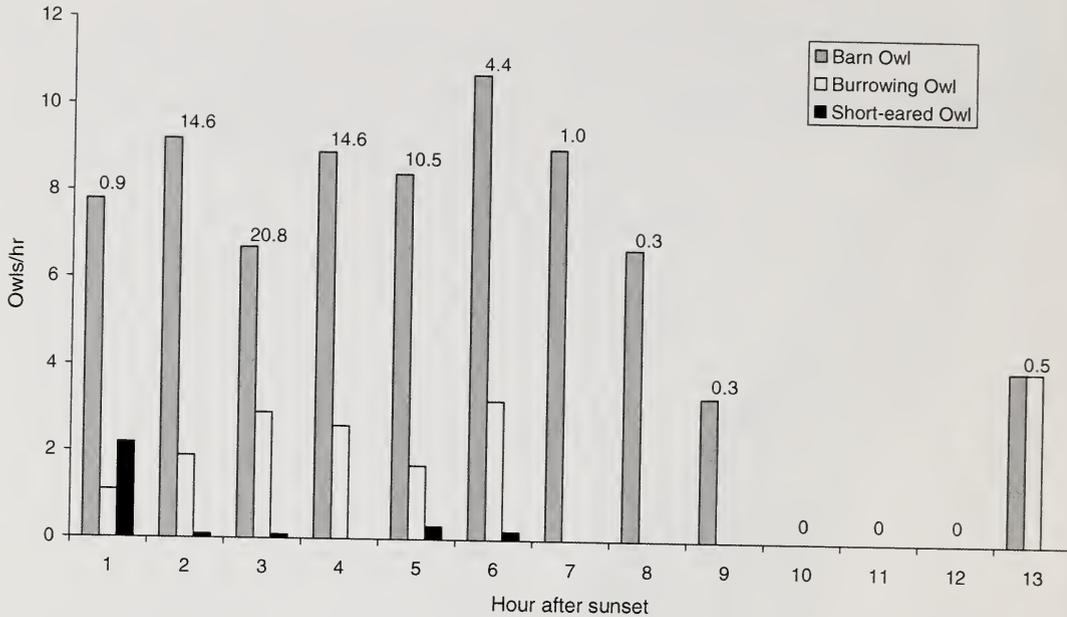


FIG. 2. Barn, Burrowing, and Short-eared owl detections/hr during 1-hr blocks after sunset for spotlighting surveys on San Clemente Island, California, 2001 and 2002. Survey effort (total hr surveyed) shown above bars.

number of owl detections/hr of effort surveyed for each time block. The number of detections/hr represents relative abundance rather than the number of individuals, as any one owl might have been observed on more than one occasion on a given night, despite our efforts to reduce double counting. Means are presented  $\pm$  SE.

## RESULTS

We completed 68 survey hr on 104 transects (i.e., 8 transects surveyed 13 times). The mean number of transects surveyed per night was  $2.9 \pm 0.25$  (range = 1–8). Most of our survey efforts were between 2 and 6 hr after sunset ( $n = 64.9$  hr, 96%). Each transect required 30–70 min (mean completion time = 39.2 min) to survey, depending on road conditions and the number of owls observed.

*Presence/absence.*—During 13 surveys, we recorded 733 owl detections of three species: Barn ( $n = 561$ ), Burrowing ( $n = 161$ ), and Short-eared ( $n = 11$ ) owls. We detected Barn Owls on 89 of 104 (85.6%) transects, Burrowing Owls on 47 (45.2%), and Short-eared Owls on 9 (8.6%). We did not detect any owls on 8 of 104 (7.7%) transects.

*Relative abundance.*—We recorded a mean of  $8.3 \pm 0.8$  Barn Owl detections/hr (range =

3.3–10.7) over the course of the study. We consistently detected Barn Owls 1–8 hr after sunset, despite varying levels of effort (Fig. 2), and detected the fewest Barn Owls/hr 9 and 13 hr after sunset. Almost half (46%, 259 of 561), of all Barn Owl observations were on transects R4 and R5. For all months, we detected  $2.2 \pm 0.7$  (range = 0–4.0) Burrowing Owls/hr; excluding months when Burrowing Owls were presumably absent from the island, we detected  $4.0 \pm 0.6$  per hr. Burrowing Owl activity was limited to 1–6 hr after sunset or early morning hours (i.e., 13 hr after sunset; Fig. 2). We observed 68% of the Burrowing Owls on transect R1, R2, and R3. We detected  $0.2 \pm 0.1$  (range = 0–2.2) Short-eared Owls/hr for all months, and  $0.4 \pm 0.3$  per hr excluding months when this species was presumably absent from the island. We detected Short-eared Owls between 1 and 6 hr after sunset and on all transects except R7.

We observed Barn Owls every month of the year, which supports previous breeding records. We observed the greatest number of Barn Owls/hr in June and the fewest in October 2002 (Fig. 3). Burrowing Owls were observed only from October 2001 to March 2002 and in October 2002; during those times, they were detected on 84% (47/56) of the

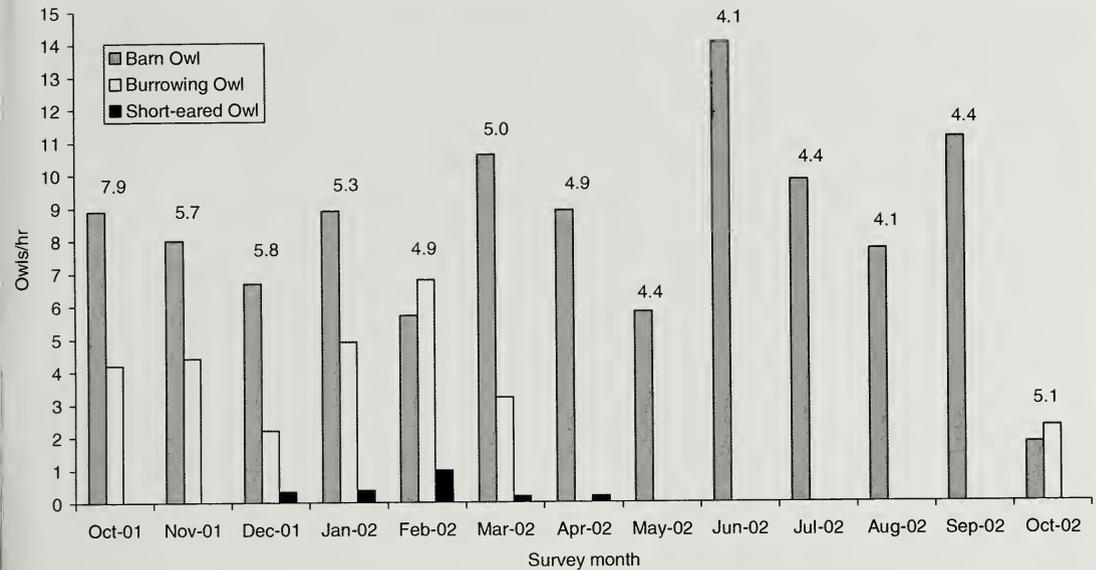


FIG. 3. Barn, Burrowing, and Short-eared owl detections/hr by month for spotlighting surveys on San Clemente Island, California, October 2001–October 2002. Survey effort (total hr surveyed) for each month shown above bars.

transects. Their absence between April and September indicates that they are primarily winter visitors. We observed Short-eared Owls on five occasions between 12 December 2001 and 7 April 2002.

**Owl behavior.**—Forty-seven percent of the Barn Owls were first detected in flight ( $n = 262$ ), and 53% were perched ( $n = 299$ ). Barn Owls perched primarily on utility wires ( $n = 157$ , 53% of perched observations), but also were seen on power poles, fences, junk piles, buildings, rocks, signs, shrubs, the ground, and the road ( $n = 89$ ). Burrowing Owls were detected both in flight (32% of detections,  $n = 51$ ) and when perched (68%,  $n = 110$ ). Burrowing Owls were most commonly found on dirt/gravel roads ( $n = 66$ ), but they also perched on utility wires, junk piles, rocks, and the ground ( $n = 18$ ). We observed 73% ( $n = 8$ ) of Short-eared Owls in flight, compared with 27% ( $n = 3$ ) that were perched.

#### DISCUSSION

We detected all three species of grassland owl on SCI, and our data suggest that SCI is an important wintering ground for each species. We found Barn Owls year-round suggesting resident status, whereas Burrowing and Short-eared owls appear to be winter res-

idents only. Burrowing Owls were the second most common species detected October through March; we recorded no detections during the breeding season. Burrowing Owls from northern breeding grounds migrate south in September and October and north in March and April (Haug et al. 1993), consistent with when we observed them on SCI. Occurrence of Short-eared Owls is irregular; they arrive in large numbers and winter on SCI only during certain years (BLS and ELK unpubl. data).

The importance of SCI for wintering owls brings up an important question: how will the natural succession of grassland habitat (in the absence of feral grazers) impact Barn, Burrowing, and Short-eared owls on SCI? As the grasslands become shrubbier, reverting to a more natural “pre-grazing” condition, we anticipate some impacts on wintering owl populations, as all three species prefer large, open grassland habitats with little shrub or tree cover (Marti 1992, Haug et al. 1993, Holt and Leasure 1993). Burrowing Owls use short-structured vegetation, including uncultivated fields, for foraging (Haug and Oliphant 1990)—presumably due to increased visibility of prey in those types (Konrad and Gilmer 1984). Reforestation (i.e., succession in this

case) generally constitutes habitat loss for Short-eared Owls (Holt and Leasure 1993).

*Owl behavior.*—All three species are thought to be primarily crepuscular foragers, especially in winter (Marti 1992, Haug et al. 1993, Holt and Leasure 1993). However, we found that all three species were active during the first 8 hr after sunset. Barn Owls appear to be active during all hours of the night. It is more difficult to assess Burrowing Owl activity because, during the months when this species was detected, we surveyed only 8 of the 13 1-hr blocks after sunset. It appears that Burrowing Owls are equally active in early morning (13 hr after sunset) and early evening hours (Fig. 2). We detected Short-eared Owls primarily in the first hour after sunset.

On SCI, Barn Owls regularly use power lines for perching, and they may be drawn to roadsides where other man-made structures serve as perches. Barn Owls are well adapted to using urban landscapes and have a habit of hunting near roads, especially in winter (Konig et al. 1999). Over half of all Barn Owls detected were perched, and of these, 53% were on utility wires. The transects with the most Barn Owl observations were situated along the main road, and utility poles are situated along its entire length.

We detected the majority of Burrowing Owls on dirt/gravel roads, where they might be attracted to the bare ground in an otherwise dense, grassy habitat. Burrowing owls are known to forage in uncultivated fields (Haug et al. 1993) and along the edges of roads (Gervais et al. 2003). Sixty-eight percent of all Burrowing Owls detected were perched on the ground, 60% of which were on dirt/gravel roads. Burrowing Owls appear to forage along or perch on dirt/gravel roads more than paved roads. We detected them most often on three transects, approximately 66% of which were dirt/gravel roads ( $n = 17$  km). Unlike larger grassland owls, Burrowing Owls forage primarily on the ground and are not as visible in flight (Haug et al. 1993).

*Use of spotlighting as a survey technique for grassland owls.*—Spotlighting is a widely used technique for surveying multiple wildlife taxa at night (e.g., mammals [Focardi et al. 2001], spiders [Martin and Major 2001], and reptiles and amphibians [Corben and Fellers 2001]). Spotlighting has been used to locate

roosting birds in forest habitats (Lindenmayer et al. 1996), as well as roosting seabirds and waterfowl (Snow et al. 1990, King et al. 1994, Whitworth et al. 1997). Debus (1995), however, found that spotlighting without audio cues while driving between survey points was ineffective for detecting forest owls.

We believe that spotlighting is an appropriate method for surveying grassland owls because these species use mostly open habitats and are visible at night while foraging (i.e., low quartering flight over vegetation or scanning for prey while perched). Furthermore, most grassland owls are light colored on their ventral side, improving detection when illuminated (Marti 1992, Holt and Leasure 1993, Marks et al. 1994). Grassland owls are typically less vocal than forest owls, especially outside of the breeding season, making traditional call-playback techniques less effective in winter (Heintzelman 1965, Haug et al. 1993, Holt and Leasure 1993, Marks et al. 1994, Toms et al. 2001, Conway and Simon 2003).

Using high-powered spotlights, we were able to efficiently survey a large proportion of SCI's grassland habitat for foraging owls. The alternative to roadside spotlighting—hiking across rugged terrain at night—would have taken substantially longer. A study comparing three survey techniques for Burrowing Owls indicated that line-transect surveys are the least effective means of surveying in the breeding season (Conway and Simon 2003). Thus, spotlighting for owls during roadside surveys might give us the best chance to cover a large area with the least number of observers while collecting valuable data.

We believe spotlighting may be useful for determining the status of owls where they are potentially at risk, or where data are lacking, especially during the non-breeding season when these species might not be as responsive to tape playback methods (Haug et al. 1993). Spotlighting might be a useful tool in estimating presence/absence in any open area, during any time of year. It might be especially useful to conduct statewide surveys, especially in the Midwestern and western United States, where long stretches of road cut through open habitat suitable for these species. This technique may also be used to quickly locate regularly used areas or ascer-

tain periods of activity for more intensive monitoring or research efforts.

Potential drawbacks to spotlighting surveys are (1) road noise, (2) the possibility of mistaking spotlighting for illegal poaching, and (3) being limited to habitat adjacent to roads, which may not accurately represent overall habitat and may inflate or decrease detection depending on species (Bart et al. 1995, Keller and Scallan 1999). In our study, we found increased detectability (possibly due to increased abundance) near roads for Barn and Burrowing owls, which may be influenced by the increased number of perches and the fact that most roads were dirt. Thus, the potential biases, as well as safety issues, associated with roadside surveys should be thoroughly evaluated prior to using this technique in other situations.

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## FERRUGINOUS PYGMY-OWLS: A NEW HOST FOR *PROTOCALLIPHORA SIALIA* AND *HESPEROCIMEX SONORENSIS* IN ARIZONA

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**ABSTRACT.**—While banding Cactus Ferruginous Pygmy-Owls (*Glaucidium brasilianum cactorum*) in Arizona, we removed three *Protocalliphora sialia* (Diptera: Calliphoridae) from the wing margin of one nestling. Subsequent inspection of nest material revealed an additional 119 *Hesperocimex sonorensis* (Hemiptera: Cimicidae), another hematophagous parasite. All nestlings ( $n = 3$ ) fledged successfully, but on day 8 postfledging, two fledglings were found dead and one was missing. Although unsubstantiated, the subclinical effect (e.g., anemia) of these hematophagous parasites may have contributed to the fledglings' demise. This is the first published record of *P. sialia* parasitizing Ferruginous Pygmy-Owls and the first documented infestation of *H. sonorensis* for nesting Ferruginous Pygmy-Owls. Received 2 August 2004, accepted 23 February 2005.

Cactus Ferruginous Pygmy-Owls (*Glaucidium brasilianum cactorum*, hereafter pygmy-owl) are secondary obligate cavity nesters that require mature trees, including large columnar cacti, for nesting (Proudfoot and Johnson 2000). In March 1997, the U.S. Fish and Wildlife Service listed the pygmy-owl as endangered in Arizona (U.S. Fish and Wildlife Service 1997). In 1999, only 41 adult pygmy-owls were known to exist in Arizona. In 2000 and 2001, population sizes in Arizona were 34 and 36 adults, respectively (U.S. Fish and Wildlife Service 2003).

On 2 June 2002, during a cooperative study of nesting ecology and phylogeography of pygmy-owls in Arizona, we removed three dipteran larvae from the right wing of one pygmy-owl nestling. Larvae were incidentally discovered and then removed during routine banding of nestlings. The larvae, later identified by T. L. Whitworth as *P. sialia* (Diptera: Calliphoridae), were on the wing margin between secondary remiges number 5 and 6, 6 and 7, and 10 and 11. We preserved larvae in 95% ethanol and vouchered samples as study specimens at the Texas Cooperative Wildlife Collection at Texas A&M University in College Station. Subsequent examination of the infested nestling's siblings revealed no addi-

tional ectoparasites. To the best of our knowledge, this is the first record of *P. sialia* parasitizing pygmy-owls.

The nest cavity was 3.5 m above ground level in a saguaro cactus (*Carnegiea gigantea*) in the Altar Valley southwest of Tucson, Arizona. The entrance diameter ( $7.5 \times 9.0$  cm) was large enough to remove nestlings and nest material by hand. After the nestlings fledged, we removed and examined nest material for additional *P. sialia*; none were found. However, we did collect 119 *Hesperocimex sonorensis* (Hemiptera: Cimicidae), another hematophagous parasite. To the best of our knowledge, this is the first published record of *H. sonorensis* infesting a pygmy-owl nest cavity. Due to funding and time limitations, nest material was not examined from any other pygmy-owl nest cavities.

The Calliphoridae mostly comprise necrophagous fly species that, in the larval stage, consume carrion or decaying flesh in wounds, and are generally known as blow flies (Mullen and Durden 2002). Larval *Protocalliphora*, however, are hematophagous parasites that commonly feed on nestlings of nidicolous birds (Hill and Work 1947, Bohm 1978, Bolland et al. 1989, Merino and Potti 1998). Few studies have shown a direct link between *Protocalliphora* infestations and nestling mortality or reductions in nest productivity (Gold and Dahlsten 1983, Roby et al. 1992). However, recent studies have found evidence of indirect links between hematophagous parasites and nestling-to-fledgling survival. For example, in House Wrens (*Troglodytes aedon*)

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a >25% loss in hemoglobin levels was attributed to blood feeding by *P. parorum* and *Dermanyssus hirudinis* (a mite; Acari: Mesostigmata: Dermanyssidae). A hemoglobin deficiency of this magnitude may significantly reduce the transport of oxygen to tissues. If fledglings retain low hemoglobin and oxygen levels, their anemic state may have a negative effect on the birds' survivorship by reducing the ability to sustain flight and escape predators (O'Brien et al. 2001). In Blue Tits (*Parus caeruleus*), there was a strong negative correlation between the heritability of chick body size and *Protocalliphora* infestation, as young of infested nests produced offspring with a shorter than average tarsus (Charmantier et al. 2004).

The Cimicidae includes about thirty species of blood-feeding ectoparasites world wide. In birds, infestation of *Oeciacus vicarius* was attributed to the abandonment of nest houses used by adult Purple Martins (*Progne subis*), and to the death of 10 nestlings that fledged prematurely (Loye and Ragan 1991). In Nebraska, high infestation of *O. vicarius* was credited with reduced body condition and seasonal decline in reproductive success of Cliff Swallows (*Petrochelidon pyrrhonota*; Brown and Brown 1986, 1999). Continued study showed that parasitized nestlings had increased asymmetry in wing and tail feathers, possibly due to nutritional stress resulting from blood loss. Feather asymmetry may impair flight performance and reduce foraging efficiency, a possible fitness cost to Cliff Swallows (Brown and Brown 2002). In New Mexico, infestation of *Haemosiphon inodorus* was credited with the abandonment of one Prairie Falcon (*Falco mexicanus*) nest (three eggs), and with the death of seven Prairie Falcon (broods of three and four) and two Red-tailed Hawk (*Buteo jamaicensis*) nestlings (Platt 1975).

We know of no studies citing *Protocalliphora* or Cimicidae infestation as the cause of a significant reduction in overall numbers of any avian species; thus, it is likely that a co-existence has developed between parasite and host (Gold and Dahlsten 1983). However, we would not rule out the possibility that heavy hematophagous parasite infestations may be detrimental to populations of species with low

numbers that are under extreme environmental stress.

The three nestlings banded on 2 June 2002 were monitored to fledging (15 June) and for 8 days postfledging. Eight days postfledging, the nestling from which we removed the *P. sialia* was found dead at the base of a saguaro cactus. The carcass was intact with no sign of depredation or scavengery. That same day, another fledgling was found dead. The carcass was found in a saguaro cavity, and plucked feathers were visible at the entrance. AGF (Arizona Game and Fish Department) researchers could not determine whether the nestling was depredated or if it had died and then was scavenged. A concentrated effort (~1 hr) by six researchers failed to locate the remaining fledgling. AGF researchers returned to the nest area on three occasions and could not locate the third fledgling (D. J. Abbate pers. comm.). Because pygmy-owl fledglings do not disperse from their natal area until ~56 days postfledging (Proudfoot and Johnson 2000; GAP pers. obs.), AGF researchers assumed the remaining fledgling was also dead. Although pygmy-owls commonly reuse nest cavities (Weidensaul 1989), this nest cavity was not active during the next season (2003; D. J. Abbate pers. comm.). Notably, Cliff Swallows avoid nesting in areas with previously high infestation levels of *O. vicarius* (Brown and Brown 1992).

There is no direct evidence that parasitic blood loss had an effect on the survival of these pygmy-owls. It is possible that drought conditions in the Tucson Basin during 2002 (<http://www.wrh.noaa.gov/twc/climate/seazDM.php>) were a contributing factor. However, after reviewing recent research on *Protocalliphora* and Cimicidae, we would not rule out parasitic blood loss as a factor contributing to the mortality of these fledglings. Using hand removal of nest material, we collected 119 *H. sonorensis* (~40/nestling). Average infestation of *O. vicarius* in Barn Swallow and Cliff Swallow nests was 19 and 32/nestling, respectively (Orr and McCallister 1985). Brown and Brown (1992) reported averages of 199 and 565 *O. vicarius*/nest site. Assuming we collected 100% of the ectoparasites from the nest cavity, the parasite load (~40/nestling) we report exceeded levels reported by Orr and McCallister (1985), but it

was considerably less than the deleterious infestation levels reported by Brown and Brown (1986, 1992, 2001, 2003). Cimicidae, however, are considered nocturnal and are known to crawl into cracks and crevices during daylight (Usinger 1966). Thus, extracting nest material by hand during daylight most likely provided a conservative representation of *H. sonorensis* infestation. Hand removal of nest material also may have resulted in failure to extract mobile *P. sialia* larvae or puparia that were located in cavity crevices. In addition, as poikilothermic organisms, the growth rate of *Protocalliphora* is essentially a function of temperature (growth rate increases linearly with temperature; Adams and Hall 2003). Thus, with an average daily high temperature of  $>30^{\circ}\text{C}$  during May and June in Tucson, Arizona (<http://wc.pima.edu/Bfiero/tucsonecology/climate/stats.htm>), we suspect that the life cycle of *P. sialia* in the Altar Valley of the Sonoran Desert is at or near the 18-day minimum for the species (Sabrosky et al. 1989). Because its life cycle in Arizona may be considerably shorter than the average time nestling pygmy-owls spend in the nest cavity (28 days; Proudfoot and Johnson 2000), it is possible that multiple *P. sialia* parasitized pygmy-owl nestlings, completed their life cycle, and left the cavity as adults before we extracted nest material. Regrettably, we did not search nest material for pupal cases.

The effect of hematophagous parasites on pygmy-owl productivity and nestling survival is not known and additional study is needed to assess the potential impact of these parasites on the endangered pygmy-owls of Arizona. The intent of this paper was to increase awareness of the parasitic association of *P. sialia* and *H. sonorensis* and pygmy-owls, and to raise the possibility of postfledging mortality attributable to these parasites.

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## EXTREMELY LOW NESTING SUCCESS AND CHARACTERISTICS OF LIFE HISTORY TRAITS IN AN INSULAR POPULATION OF *PARUS VARIUS NAMIYEI*

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**ABSTRACT.**—Differing intensities of predation pressure can affect the evolution of life history traits in island and mainland populations. We found extremely low nesting success in an insular subspecies of the Varied Tit (*Parus varius namiyei*; Kozushima Island), and we compared certain life history traits among three subspecies of *P. varius* experiencing different predation pressures. The nesting success of *P. v. namiyei* was extremely low as a result of significant nest predation and nest abandonment; 83% of active nests failed due to snake predation. The proportion of depredated nests was significantly greater on Kozushima Island than on Miyakejima Island (*P. v. owstoni*) or on the mainland (*P. v. varius*). Of the three subspecies, *P. v. namiyei* had the longest incubation period, shortest nestling period, an intermediate clutch size, and a small brood size. There were no differences in the date of egg laying among the three populations. The short nestling period for *P. v. namiyei* may be an adaptive response, as the predation risk during the nestling period on Kozushima was extremely high. Received 3 August 2004, accepted 16 March 2005.

Nest predation is a major cause of nestling mortality in avian species (Ricklefs 1969, Skutch 1985, Martin 1988, Rotenberry and Wiens 1989, Weatherhead and Blouin-Demers 2004). The intensity of predation pressure can affect the evolution of life history traits (Cody 1971, Clark and Wilson 1981, Slagsvold 1982, Nilsson 1984, Stutchbury and Morton 2001), and high nest predation generally results in selection for individuals that can reduce their investment in each breeding attempt (Slagsvold 1982, Lundberg 1985). This is particularly true of small birds, which are usually unable to protect their nests against predators. Some researchers have investigated this theory by comparing island and mainland populations, because predation pressure on islands often differs from that of mainland populations (Higuchi 1976, Loiselle and Hoppes 1983, George 1987, Sieving 1992). Higuchi (1976) reported that some life history traits of one insular subspecies of the Varied Tit (*Parus varius owstoni*) differed from those of the mainland subspecies (*P. v. varius*) and that predation pressure differed between the two populations.

We report extremely low nesting success in one insular subspecies (*P. v. namiyei*) of the Varied Tit and compare certain life history traits with those of two populations studied by Higuchi (1976), each of which is subjected to different predation pressure. We also discuss whether the differences in predation pressure could be responsible for the variation in life history traits among three different subspecies of Varied Tits.

### METHODS

*P. varius* occurs on the Japanese mainland and islands, the southern Korean Peninsula, and Taiwan. The species is divided into eight subspecies across its range (Ornithological Society of Japan 2000). *P. v. varius* occurs on the mainland of Japan and the southern Korean Peninsula, *P. v. namiyei* is found on three northern islands (Niijima, Toshima, and Kozushima; Fig. 1) of the Izu Archipelago, and *P. v. owstoni* occurs on three southern islands (Miyake, Mikura, and Hachijo).

**Study site.**—The study site was Kozushima Island, Tokyo, Japan (18.87 km<sup>2</sup>; 34° 12' N, 139° 08' E; population ~2,100). The island is part of Fuji-Hakone-Izu National Park, but has a residential area that occupies about 10% of the island. The dominant vegetation is broad-leaved evergreen forest, mostly *Castanopsis cuspidate*, *Machilus thunbergii*, and second-growth *Abus sieboldiana*. Patches of cedar (*Cryptomeria japonica*) plantations are interspersed throughout the island. The climate is

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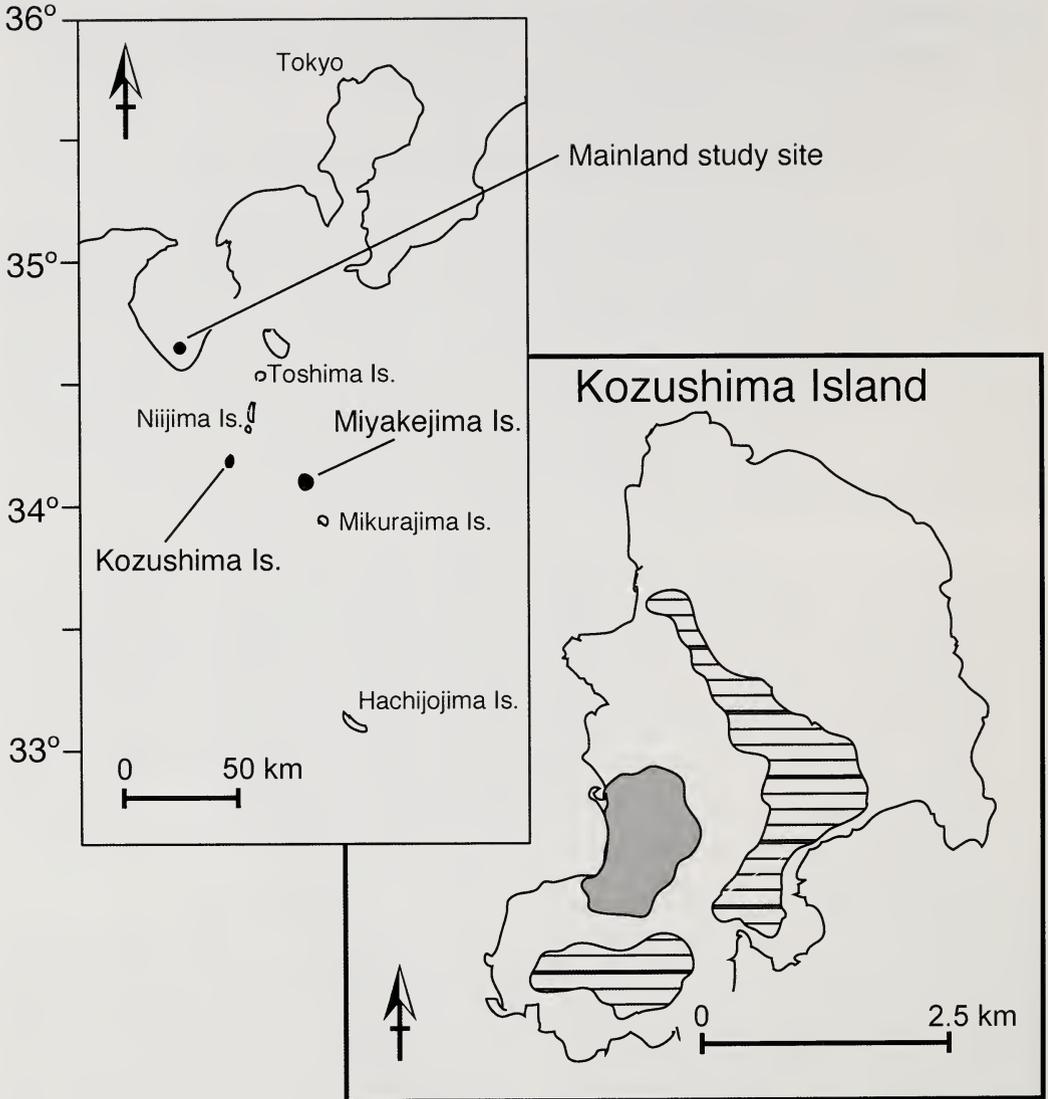


FIG. 1. Map of the Izu Archipelago and adjacent mainland of Japan, showing locations of the study sites described in both this paper and in a prior study (Higuchi 1976). The gray and hatched areas on Kozushima Island indicate the residential area and the approximate locations where nest boxes were placed, respectively.

temperate, with a mean annual rainfall of 2,535 mm and a mean annual temperature of 17.4° C. Mean temperature and rainfall on Miyakejima Island and the adjacent mainland are 16.5° C, 1,832 mm and 17.5° C, 2,907 mm, respectively (Japan Meteorological Agency, [www.jma.go.jp/JMA\\_HP/jma/indexe.html](http://www.jma.go.jp/JMA_HP/jma/indexe.html)).

*Field observations.*—We erected 137 nest boxes in 2003 and 136 boxes in 2004 (122 × 122 × 180; cavity entrance = 34 mm). Boxes were attached at a height of 2.5 m to 4–6-m

tall broad-leaved evergreen trees and 6–10-m tall planted Japanese cedars throughout the island, with the exception of the residential area and extremely steep areas. The distance between boxes was approximately 50 m. We checked each box every 3 days and recorded status, laying date, clutch size, hatching date, number of unhatched eggs, brood size, and fledging date. Our estimates of fledging date thus had a maximum possible error of 3 days; hatching date was adjusted according to de-

velopment of nestlings. We categorized predation as follows: if neither the box nor the nesting material had been damaged or disturbed, we concluded that the predator was a snake; if the entrance hole was enlarged and encircled with peck marks, we concluded that the predator was a bird (probably the Jungle Crow, *Corvus macrorhynchos*). Small, mammalian nest predators, such as martens, weasels, and squirrels, do not inhabit the island. Successful nests were defined as those from which at least one young fledged. In total, 99 of 273 boxes were used (at least one egg was laid). We attached a baffle under 48 of the 99 boxes to prevent predation by snakes; the data obtained from these boxes were excluded from calculations of predation frequency (i.e., 51 nests were used in the analyses).

*Statistical analyses.*—We calculated daily nest survival rates using the maximum likelihood method (Johnson 1979). Daily nest survival rates for the egg and nestling stages were analyzed separately. The egg period was defined as the time between the date the first egg was laid until at least one egg hatched; we defined the nestling period as the time between hatching of the first egg and fledging (Cresswell 1997). To compare daily survival rates, we used Z-tests according to the methods outlined by Johnson (1979).

Using multiple, two-tailed *t*-tests, we compared predation rates and life history traits of *P. v. namiyei* on Kozushima Island to those reported for *P. v. owstoni* and *P. varius* by Higuchi (1976) on Miyakejima Island and the mainland, respectively. We assumed that variables of life history traits followed *t* distributions, and used two-tailed Welch's *t*-tests when comparing life history traits among the three populations. We did not use ANOVA because we wanted to compare life history traits only between the Kozushima population and the other populations, and, moreover, because the variance values for all four life history traits greatly differed among populations (clutch size:  $\chi^2 = 12.05$ ,  $df = 2$ ,  $P = 0.002$ ; brood size:  $\chi^2 = 23.78$ ,  $df = 2$ ,  $P < 0.001$ ; incubation period:  $\chi^2 = 116.61$ ,  $df = 2$ ,  $P < 0.001$ ; nestling period:  $\chi^2 = 15.82$ ,  $df = 2$ ,  $P < 0.001$ ). Probability values were adjusted using sequential Bonferroni methods (Ury 1976, Sokal and Rohlf 1995). The familywise error rate was calculated as  $\alpha = 1 - (1 - 0.05)^{1/k}$ ,

where *k* is the number of tests. Adjusted *P*-values were calculated as  $P_{adj} = (0.05/\alpha) \times P$ . To compare the proportion of depredated nests, we used Fisher's exact test. We analyzed data using the software package R 1.8.1 (<http://cran.r-project.org/>).

## RESULTS

*P. v. namiyei* used 99 of 273 nest boxes (72/137 in 2003 and 27/136 in 2004); 51 of the 99 nests were used in the analyses (see Methods). Nest success (7.84%) of *P. v. namiyei* was extremely low on Kozushima Island due to nest predation and nest abandonment. Four nests were successful, 18 (35.29%) were abandoned, 19 (37.25%) were depredated, 5 (9.8%) failed because of human disturbance, and 1 (2.0%) failed due to deterioration. Four nests (7.84%) failed due to unknown causes (perhaps disease or starvation). Excluding inactive nests (abandoned, disturbed, and unknown), 82.6% (19 of 23) of active nests were depredated, all by snakes. We determined the predator species by direct observation in nine cases; all were Japanese rat snakes (*Elaphe climacophora*). Predation on a given nest was always complete (100%). Daily survival probabilities during the egg and nestling stages were  $0.991 \pm 0.002$  SE and  $0.891 \pm 0.034$  SE, respectively. The daily survival probability during the nestling stage was significantly lower than that during the egg stage ( $Z = 2.91$ ,  $P = 0.002$ ). The probability that a nest would survive through the egg and nestling stages was 0.835 (=  $0.991^{19.98}$ ) and 0.148 (=  $0.891^{16.57}$ ), respectively (Table 1).

We compared the predation pressure on Kozushima Island (*P. v. namiyei*) with that on the mainland (*P. v. varius*) and on Miyakejima Island (*P. v. owstoni*; Table 1). The proportion of depredated nests was higher on Kozushima (0.37) than on Miyakejima (0.00) or on the mainland (0.30; Fisher's exact test: Kozu versus Miyake,  $P < 0.001$ ; Kozu versus mainland,  $P < 0.001$ ). We also compared several life history traits of *P. v. namiyei*, *P. v. varius*, and *P. v. owstoni* (Table 1). *P. v. namiyei* exhibited the longest incubation period (*namiyei* versus *varius*,  $P < 0.001$ ; *namiyei* versus *owstoni*,  $P = 0.001$ ), the shortest nestling period (*namiyei* versus *varius*,  $P = 0.008$ ; *namiyei* versus *owstoni*,  $P < 0.001$ ), an intermediate clutch size (*namiyei* versus *varius*,  $P < 0.001$ ;

TABLE 1. Predation pressure (percent depredated nests) and life history traits of *P. v. namiyei* on Kozushima Island, *P. v. varius* on the mainland, and *P. v. owstoni* on Miyakejima Island, Japan. Data for the mainland and Miyakejima are from Higuchi (1976). Standard errors of the brood size for the mainland and Miyakejima are original data by HH. Mean values  $\pm$  standard errors are shown. Figures in parentheses are sample sizes.

Traits	Kozushima	Miyakejima	Mainland
Predation pressure (%)	37.25 (51)	0.00 (46)	30.28 (109)
Incubation period (days)	15.56 $\pm$ 0.22 (34)	14.06 $\pm$ 0.03 (42)	13.95 $\pm$ 0.09 (87)
Nestling period (days)	16.57 $\pm$ 0.40 (14)	18.76 $\pm$ 0.20 (39)	18.23 $\pm$ 0.27 (71)
Clutch size	5.42 $\pm$ 0.13 (76)	3.92 $\pm$ 0.10 (52)	6.23 $\pm$ 0.08 (101)
Brood size	4.33 $\pm$ 0.19 (51)	3.78 $\pm$ 0.31 (46)	6.05 $\pm$ 0.13 (76)

*namiyei* versus *owstoni*,  $P < 0.001$ ), and a small brood size (*namiyei* versus *varius*,  $P < 0.001$ ; *namiyei* versus *owstoni*,  $P = 0.14$ ).

### DISCUSSION

The nesting success of *P. v. namiyei* on Kozushima was extremely low as a result of high levels of nest predation and nest abandonment; 83% of active nests were depredated. In all cases, the predators were snakes, probably Japanese rat snakes. We frequently found these snakes when checking nest boxes, and although no abundance data are available, we consider them to be abundant on Kozushima.

The proportion of abandoned nests was also large (0.35). Significant predation pressure may result in a relatively low threshold of tolerance before a female *P. v. namiyei* will abandon her nest. Nest abandonment and re-nesting induced by nest predation are likely subjected to strong selective pressure; thus, any decision rule may be adaptive (Bauchau and Seinen 1997). We believe that our regular nest checks did not induce abandonment. Nest abandonment rates due to human disturbance (12%) in our study were not as high as those reported in other studies of *P. varius* (15%; Yamaguchi and Kawano 2001, Yamaguchi et al. 2003).

Predation rates differed between Kozushima, Miyakejima, and the mainland, although the sites are relatively similar in terms of vegetation and climate. The differences in predation rates are probably a function of the differences in snake abundance. Snakes are absent from Miyakejima Island, and no nest predation was observed by Higuchi (1976). Japanese rat snakes are native to both Kozushima Island and the mainland.

The three subspecies of *P. varius* differed in terms of their life history traits. The nest-

ling period of *P. v. namiyei* was the shortest among the three populations. This result supports the notion that high predation levels may exert strong selection pressure on length of nestling period (Skutch 1949, Cody 1966, Lack 1968, Ansersson et al. 1980, Milonoff 1989, but see Barash 1975). This may be an adaptive response, as the predation risk during the nestling stage on Kozushima Island was extremely high. The shorter nestling period in *P. v. namiyei* may be due, in part, to a relatively small brood size (Slagsvold 1984, Bosque and Bosque 1995) or more rapid growth during the nestling phase.

Of the three subspecies, *P. v. namiyei* had the longest incubation period, and its clutch size was intermediate. These life history traits would seem to be maladaptive under the influence of high predation pressure, as birds can reduce their investment in any one breeding attempt by reducing clutch size (Perrins 1977, Ricklefs 1969, Slagsvold 1982, Lundberg 1985). However, prolonged incubation periods and undiminished clutch sizes may be related to low hatchability in *P. v. namiyei* (K. Fujita unpubl. data), which could be attributable to low nest attentiveness at crucial periods during the embryo development period.

Differences in life history traits among populations evolve in response to a number of ecological and environmental factors (e.g., longevity, mating system, food abundance, climate, and predation pressure). Of these factors, predation pressure may be one of the most important factors producing the observed differences in life history traits in the subspecies of the Varied Tit.

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# Short Communications

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## First Record of Bronzed Cowbird Parasitism on the Great-tailed Grackle

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**ABSTRACT.**—We report the first record of Bronzed Cowbird (*Molothrus aeneus*) parasitism on the Great-tailed Grackle (*Quiscalus mexicanus*), which represents the 96th known host for this cowbird species. The record is based on a parasitized clutch, collected from Sinaloa, Mexico, in the collection at the Western Foundation of Vertebrate Zoology. The clutch contained four grackle eggs and one Bronzed Cowbird egg. This record is unusual because the Great-tailed Grackle is extremely intolerant of foreign eggs, ejecting them from their nests almost immediately. As the Bronzed Cowbird expands its range and is studied in greater depth, more hosts will undoubtedly be recorded. Received 22 July 2004, accepted 19 March 2005.

The five species of brood parasitic cowbirds (*Molothrus* spp.) differ greatly in the numbers of hosts they use. Brown-headed (*M. ater*) and Shiny (*M. bonariensis*) cowbirds are known to have parasitized more than 200 hosts, while the Giant (*M. oryzivorus*) and Screaming (*M. rufoaxillaris*) cowbirds parasitize 10 host species or less (Ortega 1998). The Bronzed Cowbird (*M. aeneus*) uses an intermediate number of hosts, with a total of 95 known host species (Lowther 1995, Sealy et al. 1997, Lowther 2004). Lanyon (1992) and Rothstein et al. (2002) have discussed alternative evolutionary scenarios for the evolution of host use and the relationship between the number of hosts used by each cowbird species and its branching order in the phylogeny of cowbirds. Additional data on host use are needed to resolve these issues, especially for the Neotropical cowbird species, in part because the number of recorded hosts is influenced by various biases, such as research effort, range, and even

body size of a particular cowbird species (Rothstein et al. 2002).

The Bronzed Cowbird is one of the least studied cowbird species (but see Carter 1986, Peer and Sealy 1999b, Chace 2004) and new data on its host use are especially valuable and could lead to tests of the hypothesis that Bronzed Cowbirds are more specialized in areas where they are sympatric with Brown-headed Cowbirds (Peer and Sealy 1999b). Here, we report the first record of Bronzed Cowbird parasitism on the Great-tailed Grackle (*Quiscalus mexicanus*), representing the 96th recorded host of this cowbird species. The Great-tailed Grackle, like other grackle species, is rarely parasitized by cowbirds (Rothstein 1975, Peer and Bollinger 1997, Peer et al. 2001, Peer and Sealy 2004b), and our record represents the first recorded observation of cowbird parasitism on the Great-tailed Grackle, despite the fact that it is sympatric with four parasitic cowbird species. There is also no evidence of conspecific brood parasitism in Great-tailed Grackles (Johnson and Peer 2001).

On 16 April 2003, we discovered the parasitized clutch in the collection of the Western Foundation of Vertebrate Zoology in Camarillo, California. The clutch, which had been collected on 16 May 1882 by A. Forrer in Presidio, Sinaloa, Mexico, contained four Great-tailed Grackle eggs and one Bronzed Cowbird egg. The clutch was set mark 169,12, and catalog number 167555-1+4. The description stated that incubation was “fresh” and identity “sure.”

The number of known hosts for the Bronzed Cowbird has increased 500% since Friedmann's (1929) seminal study of the cowbirds. Our discovery of the Great-tailed Grackle as a host will likely be followed by additional host records as research is conducted in the little-studied southern portion of this cowbird's range. In addition, the grackle is expanding its range in response to habitat

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modification; thus, the species is encountering new hosts (Sealy et al. 1997). Nonetheless, the Bronzed Cowbird appears to be more restricted with respect to its host species than the Brown-headed Cowbird. Brown-headed Cowbirds parasitize more than two times as many hosts as Bronzed Cowbirds in areas where the species occur in equal numbers (Peer and Sealy 1999b).

Bronzed Cowbirds were once thought to parasitize mostly orioles (*Icterus* spp.; Friedmann 1963), but this view has changed as more hosts have been discovered. Only 10 of the 96 Bronzed Cowbird hosts are *Icterus* species, and (including our discovery) only 15% of recorded hosts are members of Icteridae. Host use appears to be influenced by community composition. For example, Peer and Sealy (1999b) found that the most commonly parasitized host in southern Texas was the Northern Cardinal (*Cardinalis cardinalis*), which was much more abundant there than orioles.

This is the first recorded observation of parasitism on Great-tailed Grackles—probably due to the species' anti-parasite behaviors. The Great-tailed Grackle is 1 of only 30 species in North America known to regularly eject cowbird eggs (Peer and Sealy 2004a) and they are extremely intolerant of foreign eggs. Not only do they reject 100% of experimental Bronzed and Brown-headed cowbird eggs (typically within hours), they also reject conspecific eggs that closely resemble their own (Peer and Sealy 2000, Peer and Sealy 2004b). Thus, cowbird parasitism may go largely undetected because the cowbird eggs are ejected before researchers ever see them. However, Peer and Sealy (1999b, 2004b) monitored 798 nests daily, beginning just before sunrise when Bronzed Cowbirds lay their eggs (Peer and Sealy 1999a), and found no evidence of parasitism, suggesting that cowbirds avoid parasitizing grackles because their eggs would be ejected.

The lack of parasitism is not due to the grackle's larger size. Similar to Shiny and Giant cowbirds, Bronzed Cowbirds parasitize hosts larger than themselves more often than do Brown-headed Cowbirds. Despite having only 57% of the mass of Great-tailed Grackle hatchlings, cross-fostered Bronzed Cowbirds can fledge from Great-tailed Grackle nests, in-

dicating that the grackle is a suitable host species (Peer and Sealy 2004b).

This observation supports Peer and Sealy's (2004b) hypothesis that Bronzed Cowbird parasitism may have exerted selection pressure on the egg-ejection behavior demonstrated by Great-tailed Grackles. On the other hand, it may be more likely that this ejection behavior evolved in response to parasitism by the Giant Cowbird, the eggs of which closely resemble grackle eggs, and which also specializes on parasitizing large, colonial members of the Icteridae (Peer and Sealy 2004b).

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## A Cause of Mortality for Aerial Insectivores?

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**ABSTRACT.**—A male Eastern Phoebe (*Sayornis phoebe*) was found dead on 15 April 2004, hanging from a piece of monofilament fishing line over the Kinnikinic River near River Falls, Wisconsin (Pierce County). The individual was hooked through the tongue by a fly-fishing lure. Although fishing tackle has been reported as a cause of mortality for several aquatic bird species, further research is needed to determine whether abandoned trout-fishing lures represent a significant threat to aerial insectivores. *Received 13 September 2004, accepted 28 February 2005.*

The Eastern Phoebe (*Sayornis phoebe*) is a subsocial flycatcher (Tyrannidae) that breeds throughout the eastern United States and southern Canada. It is one of the earliest migrants to return in the spring (Weeks 1994). Eastern Phoebes are primarily aerial insectivores, but they also glean insects from a variety of substrates (Via 1979). They feed primarily in edge habitats (Weeks 1994), including along stream banks where they fly out over the water to capture prey. Flying insects compose the majority of the Eastern Phoebe's diet (Weeks 1994). During hatches of insects

from streams, individuals often forage low over the water by hawking (MDE pers. obs.). Eastern Phoebes also have been observed catching fish, sometimes hovering over the water for several seconds before taking the prey (Binford 1957).

On 15 April 2004, a male Eastern Phoebe (sex was subsequently determined by inspection of gonads) was found dead, hanging approximately 0.5 m below a tree branch that was 2 m above a small river (Fig. 1). We found the bird ~0.8 km downstream from the River Falls dam on the Kinnikinic River near River Falls, Wisconsin (Pierce County). Closer inspection revealed that the Eastern Phoebe was hanging from the end of a piece of monofilament fishing line. We recovered the bird on 16 April and deposited it at the Bell Museum of Natural History at the University of Minnesota (catalogue #MDE-065).

The phoebe was hooked through the tongue by a fishing lure used for fly-fishing. Presumably the line was broken off once it and the lure became entangled in the tree. The lure was a bead-head pheasant-tail nymph, which generically mimics the larval stage of mayfly species (Ephemeroptera). These larvae are aquatic, thus, this lure does not mimic the normal aerial insects that typically compose the Eastern Phoebe's diet. We hypothesize that the lure was bouncing around at the end of the

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FIG 1. Eastern Phoebe (*Sayornis phoebe*), attached to monofilament fishing line and lure, hanging from a tree branch over the Kinnikinic River, River Falls, Wisconsin, 15 April 2004.

line on a windy day and appeared to the phoebe as a flying insect. The bird then caught the lure in its bill, and the hook pierced the tongue. An alternative hypothesis is that this individual was trying to collect the fishing line to use as nesting material, but happened to grab onto the lure and got hooked. Eastern Phoebes have been previously reported tangled in fishing line and twine that were being used as nesting material (Clapp 1993, Friesen 2002). Use of man-made materials in passerine nests is a widespread phenomenon, as many species will use whatever materials are readily available (Baicich and Harrison 1997). Paper, string, and plastics are commonly reported as nesting materials used by species living in, or near, urban areas (e.g., Lowther

and Cink 1992, Cabe 1993, Rising and Flood 1998).

This is the first time that this source of avian mortality has been reported. We could find no estimates in the literature of the number of fly-fishing lures per km of stream; thus, we have no way to estimate the rate of mortality by these lures on birds, but typical trout-fishing outings often result in the loss of several lures due to entanglement with streamside trees and shrubs (MDE and DLH pers. obs.). Additional research is needed to determine whether Eastern Phoebes and other aerial insectivores commonly mistake fly-fishing lures for food, and how frequently such lures are found along trout streams.

Research on aquatic birds has shown that

fishing tackle (i.e., fishing hooks, lures, line, and lead weights) can be a significant source of mortality in some species. In particular, the consumption of lead weights and lead portions of fishing tackle accounted for 10–50% of adult mortality in two different studies of Common Loons (*Gavia immer*; Scheuhammer and Norris 1996, Sidor et al. 2003), and ingestion of lead weights was the single largest cause of death in several populations of Mute Swans (*Cygnus olor*) in Great Britain (Kirby et al. 1994). In addition, high rates of ingestion of non-lead portions of fishing tackle have been reported in Brown Pelicans (*Pelecanus occidentalis*; Franson et al. 2003). Franson et al. (2003) concluded that portions of fishing tackle exclusive of lead weights contributed to mortality, not only in Brown Pelicans, but also in Common Loons, Black-crowned Night-Herons (*Nycticorax nycticorax*), Bald Eagles (*Haliaeetus leucocephalus*), and Double-crested Cormorants (*Phalacrocorax auritus*). Apart from the species mentioned above, documented cases of non-lead fishing tackle as a source of avian mortality are extremely few.

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## First Record of Swainson's Warbler Parasitism by *Protocalliphora* Blow Fly Larvae

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**ABSTRACT.**—We report the first record of blow flies (*Protocalliphora*) parasitizing Swainson's Warblers (*Limnothlypis swainsonii*). Eight of 12 (67%) nests collected in southeastern Oklahoma during four breeding seasons (2001–2004) were parasitized by *P. deceptor* larvae. Because Swainson's Warbler is considered a species of high conservation priority in the southeastern United States, and because *Protocalliphora* can have negative impacts on their hosts, factors influencing blow fly parasitism of this species warrant further investigation. Received 27 February 2004, accepted 16 March 2005.

*varia gigantea*), Japanese honeysuckle (*Lonicera japonica*), and other substrates. Swainson's Warblers are single brooded and lay a clutch of 2–5 eggs (mean = 3.3); only the female broods and clutches hatch in 13–15 days (Brown and Dickson 1994). The average nestling period for Swainson's Warblers in our study was 10 days.

Swainson's Warbler (*Limnothlypis swainsonii*) is one of North America's most secretive avian species, and little is known about many aspects of its biology, including parasites and disease (Brown and Dickson 1994). Here, we present the first information regarding parasitism by *Protocalliphora* blow flies in this species. Larvae of *Protocalliphora* (Diptera: Calliphoridae) are obligate hematophagous parasites that reside in the nests of birds with nidicolous young. To feed, larvae of most species attach intermittently to the nestlings. Effects of this parasite on their avian hosts range from little or none (e.g., Miller and Fair 1997) to reduced hematocrit and hemoglobin levels (Whitworth and Bennett 1992), slowed growth and development (e.g., Johnson et al. 1991, Hurtrez-Bousses et al. 1997), reduced activity (Bergtold 1927), reduced adult survival (Wesolowski 2001), and death (Halstead 1988).

Swainson's Warblers are monomorphic, Neotropical migrants that breed in bottomland hardwood forests in the southeastern United States. During our study, nests were located in dark, densely vegetated areas near water in greenbriar (*Smilax* spp.), giant cane (*Arundi-*

We conducted our study at Little River National Wildlife Refuge (LRNWR) in McCurtain County, Oklahoma (33° 56' N, 94° 42' W). LRNWR is located in the floodplain of the Little River (elevation 102 m) and is composed primarily of bottomland hardwood forest interspersed with sloughs and drainages. We located Swainson's Warblers nests by systematically searching appropriate habitat (Meanley 1971) in and near identified male territories. Nests were monitored from 30 April to 24 July 2001–2004, following protocols outlined in Martin and Geupel (1993). At the end of each breeding season, we collected nests and examined them for *Protocalliphora* pupae and adults, which were then identified to the species level. Only nests that had contained nestlings at least 6 days old were examined; *Protocalliphora* larvae do not pupate until they reach the third instar and pupae will not form when nestlings are younger than 6 days. Of nests ( $n = 12$ ) that contained nestlings  $\geq 6$  days old, 33% (1/3) were parasitized in 2001, 50% (1/2) in 2002, 80% (4/5) in 2003, and 100% (2/2) in 2004. Hatch date, number of nestlings and pupae, and nest fate are shown in Table 1. Two additional nests located in 2002 and 2003 after the nesting attempts had been completed also were parasitized, but are not included because age and fate of nestlings was not known. The first was located 4 June 2002 and contained 10 pupae, and the other was located 23 June 2003 and contained 3 pupae. All 14 nests were parasitized by *P. deceptor*, a generalist species that infests the nests of many species in the eastern United States.

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TABLE 1. The number of parasitic *Protocalliphora* larvae found in Swainson's Warblers nests does not appear to be related to number of nestlings or presence of Brown-headed Cowbird nestlings. A greater proportion of unparasitized nests with known fates (3/3) were successful (fledged young) than parasitized nests (6/8). Nests in which young hatched later in the breeding season (after 28 May,  $n = 6$ ) had a greater prevalence of parasitism (83%) than those hatching earlier (50%,  $n = 6$ ). Only nests that contained nestlings  $\geq 6$  days old were considered (*Protocalliphora* pupae do not form when nestlings are younger than 6 days). Nests were collected at the Little River National Wildlife Refuge, McCurtain County, Oklahoma, 2001–2004.

Hatch date	No. nestlings	Nestling age (days) <sup>a</sup>	No. pupae	Nest fate
17 May 2001	1	10	—	Fledged
18 May 2001	4	9	—	Fledged
17 May 2001	3 <sup>b</sup>	6–8	15	Depredated
14 May 2002	1 <sup>b</sup>	$\geq 8$	—	Unknown
22 June 2002	1	10	9	Fledged
26 May 2003	2	10	4	Fledged
29 May 2003	3	10	27	Fledged
5 June 2003	3	9–10	—	Fledged
2 July 2003	2	9–10	1	Fledged
17 July 2003	3	8–10	9	Fledged
16 May 2004	4	7	17	Depredated
2 June 2004	3	9	38	Fledged

<sup>a</sup> Age of nestlings when nest either failed or nestlings fledged.

<sup>b</sup> Nest contained one Brown-headed Cowbird nestling.

Swainson's Warbler is ranked high on lists of avian species of special concern (Louisiana Nature Conservancy 1992, Hunter et al. 1993, Smith et al. 1993, Thompson et al. 1993). Information about factors influencing reproductive success of Swainson's Warblers, such as *Protocalliphora* parasitism, is important for developing appropriate conservation strategies.

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## First Record of Eurasian Jackdaw (*Corvus monedula*) Parasitism by the Great Spotted Cuckoo (*Clamator glandarius*) in Israel

Motti Charter,<sup>1,4</sup> Amos Bouskila,<sup>2</sup> Shaul Aviel,<sup>3</sup> and Yossi Leshem<sup>1</sup>

**ABSTRACT.**—Little is known about the biology of the Great Spotted Cuckoo (*Clamator glandarius*) in Israel. After erecting nest boxes intended for cavity-nesting raptors, however, we had opportunities to observe Great Spotted Cuckoos parasitizing Eurasian Jackdaws (*Corvus monedula*) that also nested in some of the boxes. During the 2003 breeding season, we monitored seven jackdaw nests, six of which were parasitized by cuckoos. In five of the jackdaw nests, one to four cuckoo eggs hatched, and one to three nestlings survived to fledge (four nests). This is the first documentation of Great Spotted Cuckoos parasitizing jackdaws in Israel. Received 4 June 2004, accepted 18 February 2005.

The Great Spotted Cuckoo (*Clamator glandarius*) is an obligate brood parasite. In Europe, the cuckoo's main host is the Common Magpie (*Pica pica*), and the Carrion Crow (*Corvus corone*) serves as a secondary host (Cramp 1985a). Cuckoos will parasitize other corvids, both in Europe (Cramp 1985a, Soler 1990) and in Africa (Jensen and Jensen 1969, Cramp 1985a), but their breeding success is generally greater when parasitizing magpies (Soler 1990). Parasitism of Eurasian Jackdaws (*Corvus monedula*) by Great Spotted Cuckoos has been observed in Spain, but at low frequencies (Soler 1990, 2002).

In Israel, the Great Spotted Cuckoo is a summer resident, arriving from mid-December to late March, and then leaving in June after the nesting season (Shirihai 1996). In Israel, Great Spotted Cuckoos mainly parasitize Carrion Crows (Yom-Tov 1975); to a lesser extent (isolated observations) they also para-

sitize Eurasian Jays (*Garrulus glandarius*; Shirihai 1996), Fan-tailed Ravens (*Corvus rhipidurus*; Shirihai 1996), and House Crows (*Corvus splendens*; Yosef 1997, 2002). Here, we report six instances of Great Spotted Cuckoos parasitizing jackdaw nests. We monitored hatching and fledging success of cuckoos in jackdaw nests to better understand the suitability of this species as a host for Great Spotted Cuckoos.

### METHODS

The study site—an organic crop field and a date plantation (combined size = 32 ha) at Kibbutz Sde Eliyahu, Israel (32° 30' N, 35° 30' E)—was situated in the Jordan Rift Valley, 7 km from the city of Beit Shean and about 200 m below sea level. During the 2003 nesting season, we monitored five jackdaw pairs that nested in small nest boxes (50 cm wide × 30 cm long × 30 cm high; entrance 22 cm high × 15 cm wide) and two pairs that nested in large nest boxes (50 × 75 × 50 cm; entrance 25 × 15 cm). The small nest boxes, intended for Eurasian Kestrels (*Falco tinnunculus*), were erected in 1998 and attached to date palms (*Phoenix dactylifera*) at a height of 6 m above the ground; the large nest boxes, intended for Barn Owls (*Tyto alba*), were erected in 1993 in crop fields at a height of 3 m above the ground. Beginning the first week in March 2003, all nests were checked weekly using a hydraulic lift supplied by Kibbutz Sde Eliyahu. Because the jackdaw clutches were unusually large (mean clutch size in Israel is 4–5 eggs; Paz 1987), we suspected that inter- or intraspecific parasitism had taken place; but due to the similarity between jackdaw and cuckoo eggs, we were unable to identify parasites until 10 days after hatching (when feathers started showing). Although shape and color of the two species' eggs differ somewhat, we were unaware of those differences until we had confirmed that some of the nest-

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TABLE 1. Hatching and fledging success of six Eurasian Jackdaw nests parasitized by Great Spotted Cuckoos in Kibbutz Sde Eliyahu, Israel, during the 2003 breeding season.

Box no.	Number of eggs			Number of nestlings <sup>a</sup>			Number of young fledged		
	Cuckoo	Jackdaw	Both	Cuckoo	Jackdaw	Both	Cuckoo	Jackdaw	Both
1	2	5	7	1	2	3	1	0	1
2	—	—	5	1	1	2	1	0	1
4 <sup>b</sup>	—	—	9	4	4	8	—	—	—
5 <sup>c</sup>	—	—	9	2	3	5	2	—	2
8	—	—	9	4	0	4	3	0	3
37 <sup>d</sup>	—	—	—	—	—	—	—	—	—
<i>n</i>	—	—	39	12	10	22	7	0	7
Mean	—	—	7.8	2.4	2.0	4.4	1.8	0	1.8
SD	—	—	1.8	1.5	1.6	2.3	1.0	0	1.0

<sup>a</sup> Brood size is a minimum estimate due to eggs/nestlings disappearing from some nests before identification.

<sup>b</sup> Nest box was accidentally knocked down by date plantation workers on 22 April. Four live cuckoos, three starved dead jackdaws, and one starving jackdaw were in the box. All were approximately 5 days old.

<sup>c</sup> One healthy and one starving jackdaw nestling were removed for another study.

<sup>d</sup> Clutch and brood size unknown: one cuckoo and one jackdaw egg were found in this abandoned jackdaw nest (discovered on 9 May). Fate of nest unknown.

lings were cuckoos; thus, the exact number of parasite and host eggs was unknown except in box number 1. In addition, the exact time and order of parasitism (before, after, or during jackdaw laying) was unknown. We identified starving nestlings as those that were substantially smaller and weaker (i.e., could not hold head up) than other nestlings, and starving or starved (dead) nestlings as those that had empty crops. Because corvids are known to remove dead nestlings from nests (Yom-Tov 1975), and because our nest checks took place only weekly, the fate (starved, diseased, depredated, etc.) of nestlings that disappeared between visits was unknown.

## RESULTS

Jackdaws started building their nests during the first 2 weeks in March, and began egg laying about 4 weeks later; both species completed egg laying between 3 and 21 April. Cuckoo eggs were sub-elliptical with blunt ends, light bluish-green, and heavily marked with light brown spots. The eggs were similar in color and shape to the middle Great Spotted Cuckoo egg depicted in Cramp (1985a:plate 95). Jackdaw eggs were more elliptical, bluish-green, and lightly to thickly marked with dark brown spots; they were similar in color to both the left and middle jackdaw eggs depicted in Cramp (1985b:plate 76), but their shape more closely matched that of the left egg.

Cuckoos parasitized six of seven jackdaw nests (85.7%); a mean of 1.8 cuckoos fledged per parasitized nest ( $n = 4$ ; Table 1). The one unparasitized jackdaw nest had a clutch of five eggs, all of which hatched, and three of which fledged. Eggs were found missing between nest checks in nest boxes 2 and 8. In box 8, there had been nine eggs, but there were just four cuckoo nestlings on the next nest check (8 days later). In box 2, three jackdaw eggs were missing after a cuckoo and a jackdaw had hatched. We were unable to determine the fate of the missing eggs or nestlings.

## DISCUSSION

The parasitism rate and reproductive success of cuckoos we report suggests that jackdaws are suitable hosts for Great Spotted Cuckoos. Moreover, the impact of parasitism on reproductive success of jackdaws appears to be severe. The nesting success of parasitized jackdaw pairs (no jackdaws fledged at four nests) was less than that of the unparasitized pair (three jackdaws fledged). However, in Spain only 6 of 290 jackdaw nests were parasitized (2.1%; Soler 1990) and only 1 of 9 parasitized nests fledged cuckoos (11.1%; Soler 2002).

Habitat characteristics may be responsible for differences in the jackdaw-cuckoo relationship in Israel versus Spain. The high rate of parasitism we observed could have been due to a lack of alternative hosts or a cuckoo

preference for jackdaw hosts. Carrion Crows nest on the kibbutz about 1 km away from our study site (they do not nest in the date plantation or crop fields themselves) and have been parasitized for the past 10 years (SA pers. obs.), but they start nesting earlier than jackdaws (late February to early March; Paz 1987). In addition, many pairs of Eurasian Jays (>20 pairs) nested in the date plantation, but we have never recorded cuckoos parasitizing the jays.

In Israel, jackdaw populations declined drastically in the 1950s due to poisoning; in 1987 they were still considered rare, nesting in just a few isolated colonies (Paz 1987). In the early 1990s, jackdaw populations started to increase, and in 1999 they began nesting in our study area (SA pers. obs.). Recent sympatry may explain the cuckoo's success in Israel, as magpies living in recent sympatry with Great Spotted Cuckoos reject fewer eggs than those living in ancient sympatry (Soler 1990, Soler and Møller 1990, Soler et al. 1999).

There were differences in nest sites and nest type used by jackdaws in Spain versus those in Israel. In Spain, jackdaws nested in colonies (2–10 individuals; Soler and Soler 1996) on clay cliffs in which there were many crevices and holes. In Israel, jackdaws nested in nest boxes located on date palms ( $n = 5$ ) and in crop fields ( $n = 2$ ). Soler and Soler (1996) found that nests with larger entrances are depredated more frequently (by Common Ravens, *Corvus corax*) and that Great Spotted Cuckoos prefer hosts that nest in trees (Soler 1990). In Israel, the large entrances of our nest boxes and the location of jackdaw nest boxes in trees may have made it difficult for the jackdaws to defend their nests.

Great Spotted Cuckoo nestlings are known to outcompete host young for food, causing the latter to starve to death (Cramp 1985a, Soler 1990, Soler and Soler 1991). In Israel, at four of five nests with data on brood size, jackdaw nestlings were found both starved and starving due to such competition. None of the cuckoo young starved. However, our findings contrast with those of Soler (2002), who found that, for the most part, Great Spotted Cuckoo nestlings, and not jackdaws, are the ones that starved in jackdaw nests.

Brood parasites may prefer certain hosts

over others. One would expect hosts that successfully raise parasitic young to be preferred over hosts that do not. In our study area, both the high rate of cuckoo parasitism of jackdaws and the cuckoo's high level of breeding success indicate that, under certain environmental conditions, jackdaws can be successful foster parents for Great Spotted Cuckoos.

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## House Wren Preys on Introduced Gecko in Costa Rica

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**ABSTRACT.**—On 25 May 2002, we observed a House Wren (*Troglodytes aedon*) eating a juvenile house gecko (*Hemidactylus frenatus*) in Golfito, Costa Rica. Just a few studies report insect-eating birds taking vertebrate prey, and we found no prior publications for this species. The recently introduced house gecko may be a new potential food resource for other native species in Costa Rica and elsewhere. Received 16 August 2004, accepted 17 March 2005.

Members of the Troglodytidae are known for their almost completely insectivorous habits. Twenty-two species of this family have been reported for Costa Rica (Barrantes et al. 2002) and they are described as incessant searchers of insects, larvae, spiders, and other invertebrates. They seek their food in forests, thickets, open groves, grasslands, and marshes. In Costa Rica, the House Wren (*Troglodytes aedon*) is commonly found around human habitations and in man-made habitats. It is a conspicuous resident species occurring from lowlands to 2,750 m, and is rarely found in extensively forested areas or dry lowlands (Stiles and Skutch 1989).

On 25 May 2002, in Golfito, Puntarenas Province, Costa Rica (08° 39' N, 83° 09' W), we observed a House Wren holding a juvenile house gecko (*Hemidactylus frenatus*) in its bill. At the onset of our observation (11:06 CST), the bird held the gecko by the neck and was perched in the upper part of a bush (Rosaceae), 1.5 m above the ground in a garden

on the campus of the Universidad de Costa Rica. The gecko was a characteristic uniform grayish-brown on the dorsum, and we estimate its size was approximately 3 cm (snout-vent length). While perched in the bush, the House Wren pounded the prey repeatedly against a branch, giving it strong shakes. Five min later, the bird flew to its nest in a nearby building with the gecko. The nest was placed about 2 m high on a beam of the open ceiling in one of the buildings' porches; the nest contained three nestlings approximately 9 to 12 days old. Finally, the House Wren fed the gecko to one of its chicks. We examined the nest but did not find a discarded gecko, suggesting that a chick ate the prey and swallowed it completely.

Cases of vertebrate predation by birds considered to be insectivorous are scarce. For example, vertebrate predation has been observed in only 4 of 50 species of wood warblers (Parulidae; Brown and Dickson 1994, Eaton 1995, Robinson 1995). Whereas there are limited reports of atypical vertebrate prey having been taken by tanagers (Aborn and Froehlich 1995, Pérez-Rivera 1997), woodcreepers, and leaf-tossers (Poulin et al. 2001), there are no such reports for wrens in Costa Rica (Stiles and Skutch 1989) or elsewhere (Guinan and Sealy 1987, Van Horne and Bader 1990, Johnson 1998). Our observation is the first report of vertebrate predation by a House Wren.

The house gecko, native to southern India, Sri Lanka, and Southeast Asia, is an invasive species that has widely extended its geographic range, and is now established in Australia, China, East Africa, and North and Central

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America (Meshaka et al. 1994, Schmidt et al. 1996). The house gecko likely invaded Costa Rica post-1990 via shipping-port activity along the Pacific coast. Despite its recent arrival, this small lizard has rapidly colonized and reached great abundance in lowland regions of Costa Rica (Savage 2002).

The widespread distribution and abundance of house geckos in and near houses and buildings potentially makes this lizard an accessible prey species for a diverse group of vertebrates. However, there are few studies that have investigated the relationship of this gecko with other native species, and how they might take advantage of this potential resource (Petren and Case 1996). There are no reports of house geckos as a food resource for any other native Costa Rican avian, mammalian, or reptilian species. Nevertheless, *H. frenatus* has an important effect on food webs by depleting insect prey for other native geckos (Petren and Case 1996). Our observation suggests that more detailed studies of the relationship between this gecko and native species are needed.

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# Ornithological Literature

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SAN DIEGO COUNTY BIRD ATLAS. By Philip Unitt. Proceedings of the San Diego Natural History Museum No. 39, Ibis Publishing, Temecula, California. 2005: 645 + vi pp., 468 color photos, several hundred maps and figures, 9 tables, 3 appendices. ISBN: 0934797218, \$80.00 (cloth).—Let this review begin with the only flaw I could find while devouring a publication that may well be the most important book about California birds since Grinnell and Miller's 1944 standard-bearer, *The Distribution of the Birds of California* (Pacific Coast Avifauna No. 27). The flaw is, simply, that its title "*San Diego County Bird Atlas*" understates the vast contributions of this effort by Unitt, several other contributing writers, and over 400 volunteers. The title might suggest that this is merely another in a worthy line of the Golden State's county-level breeding bird atlases that includes W. D. Shuford's *The Marin County Breeding Bird Atlas: A Distributional History of Coastal California Birds* (California Avifauna Series 1, Bushtit Books, Bolinas, California, 1993) and D. Roberson and C. Tenney's *Atlas of the Breeding Birds of Monterey County, California* (Monterey Peninsula Audubon Society, Carmel, California, 1993). However, in addition to being a thorough breeding bird atlas, *San Diego County Bird Atlas* also reports the results of a detailed winter atlas scheme and, furthermore, is an expanded reworking of the author's earlier publication, *The Birds of San Diego County* (San Diego Society of Natural History, Memoir 13, 1984). The Atlas thus treats all species, including transients and vagrants. It is also the most detailed and critical treatment of subspecies of southern California's birds in decades. The parochial title is an understatement, as well; although San Diego County may be geographically tucked into the far southwest corner of the United States, it boasts a bird list—493 species plus 87 additional subspecies—that is exceeded by no other county (or any region of comparable area) in the nation. This lofty total is a function of habitat and topographic diversity and

a legacy of active ornithological field work and birding activity. San Diego County lies at the heart of the southern half of the California Floristic Province and has become a key area for bird conservation issues since—as the author points out on the very first page—its human population (approaching 3 million) continues to increase at third-world rates while consuming resources at first-world rates.

San Diego County stretches from the Pacific Coast eastward over coastal hills and the Peninsular Range (to 1,990 m elevation), then down into the Colorado Desert. Its diminishing coastal sage scrub was the subject of the landmark work of Soulé et al. (Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75–92, 1988) on habitat fragmentation, and its chaparral and oak-conifer woodlands are subjected to great perturbations (some 1,715 km<sup>2</sup> of these habitats burned in 2002 and 2003, shortly after the completion of atlas field work). The county is home to a massive Marine Corps base (Camp Pendleton), Anza-Borrego Desert State Park (2,427 km<sup>2</sup>), and considerable National Forest and state park land in the mountains; there is a huge Navy presence in San Diego Bay, as well. Rapidly expanding suburban development continues in concert with important, albeit imperfect, habitat conservation planning. San Diego County is thus a robust microcosm of California and the entire nation.

This attractive and richly illustrated book begins with a detailed methodology chapter explaining the field work conducted from March 1997 to February 2002. The atlas grid is based on township/range/section boundaries, with the 479 cells averaging about 23 km<sup>2</sup>; this is a bit at odds with other California atlas efforts, but such grid differences are trivial for biogeographical analysis. After a five page summary of important results and a review of the species account format, the Atlas provides a concise summary of avian habitats, conservation issues, and impacts of wildfire. The species accounts form the bulk of the text,

with account lengths varying from a couple of paragraphs for vagrants to two to three pages for most breeding species. Maps illustrate geographical distribution of the breeding range, with abundance and certainty of breeding confirmation coded by differing intensities of green and hatching in each atlas cell. For wintering species, or species whose breeding and wintering status differ greatly, an additional map shows winter distribution (based on field work from December through February) with three shades of blue indicating abundance, based on individuals encountered per hour. Additional cells in which only migrants were recorded are shaded in gray; for some breeding species, former (pre-1997) breeding cells are colored red. Breeding species merit an additional graphic that portrays nesting phenology.

Exotic species (including a growing resident population of Black-throated Magpie-Jays, *Calocitta colliei*) and hypothetical species are treated briefly in a section subsequent to the main species accounts. There follows appendices listing all avian taxa recorded in San Diego County (most are documented by specimens in the San Diego Natural History Museum) and the scientific names of plants mentioned in the text. A third appendix provides locality data (and sometimes date) for the hundreds of color photographs; roughly half of the photos were taken in San Diego County.

Among the many strengths of the species accounts are the thoughtful Conservation sections provided for most species; population and range changes are discussed here in detail. Declines are many, but a surprising suite of species has adapted to urban and suburban habitats and expanded accordingly; these include the Red-shouldered (*Buteo lineatus*) and Cooper's hawks (*Accipiter cooperii*), Nuttall's Woodpecker (*Picoides nuttallii*), Pacific-slope Flycatcher (*Empidonax difficilis*), Western Bluebird (*Sialia mexicana*), and Dark-eyed Junco (*Junco hyemalis*). Also excellent are the critical analyses of subspecies occurring in the county; Unitt excels at a sensible and modern application of the subspecies concept, rejecting ill-supported taxa but championing "good" subspecies as illuminating ecological adaptations, endemism, and seasonal population movements.

As if the sheer amount of useful information in this book weren't enough, the author's prose is highly readable and at times strays refreshingly from stiff, scientific style. His nearly 20 years at the editorial helm of the journal, *Western Birds*, have clearly served him (and us) well. Praise for the author, however, should not minimize the labor, guidance, and technical expertise of many others involved in the Atlas. Production values are high throughout, and any errors are surely minimal. This attractive production, however, does carry a rather stiff price, and one can't help but think that a version without color on virtually every page might have come in at half the price and encouraged wider distribution. The bottom line, though, is that I recommend saving your personal and institutional pennies for this book—it's worth it. All birders and field ornithologists within hundreds of miles of San Diego County should have a copy. Those who are more geographically estranged from San Diego will still find great value in this work as a model atlas and regional treatment of status, ecology, and geographic variation.—KIMBALL L. GARRETT, Natural History Museum of Los Angeles County, Los Angeles, California; e-mail: kgarrett@nhm.org

#### CURASSOWS AND RELATED BIRDS.

By Jean Delacour and Dean Amadon, with an updated chapter by Josep del Hoyo and Anna Motis. Illustrated by Albert E. Gilbert. Lynx Edicions, Barcelona, Spain. 2004: 476 pp., 52 black-and-white maps and figures, 56 color plates, 6 dichotomous keys. ISBN: 8487334644. \$75.00 (cloth).—This book is a revision of one published approximately 30 years ago, also by Jean Delacour and Dean Amadon. The original was an elegant book about a cryptic and little known group of tropical birds—the Cracids. Delacour and Amadon published in that book every bit of information they came across, from notes scribbled by zoo curators to records of habitat, voice, and other important aspects of natural history scrawled during brief research trips to the native haunts of Cracids. When they wrote the book, they probably had no idea that they

were building the foundation for what would expand into a passion for an avian group on which Neotropical ornithologists would subsequently focus a large body of autecological research. Today, the IUCN/Birdlife Cracid Specialist Group (CSG) boasts a list of some 500 correspondents, many of which are “cracidologists” actively working in the field; for this band of dedicated scientists, the original book by Delacour and Amadon served as a bible, of sorts.

The revised *Curassows and Related Birds* is divided into three major parts. The first (pages 18–206) comprises the original book with black-and-white figures that appeared therein. The second part (pages 207–320) contains color plates from the Cracid section in *Handbook of the Birds of the World*, vol. 2: New World vultures to guineafowl; plates from the original book; and some updates (including 15 plates of downy young). The final part (pages 321–476) is the updated chapter by del Hoyo and Motis. Over the past decade, the CSG has published a plethora of books (approximately 1,000 pages in more than 100 chapters of four separate books in three languages), as well as a trilingual, biannual bulletin (20 volumes containing approximately 50 articles to date); the updated chapter is primarily an exhaustive compilation of those works.

One problem with this book is that some of the information already published by the CSG was incorrectly summarized in the chapter by del Hoyo and Motis. For example, in a discussion of the Chaco Chachalaca (*Ortalis canicollis*) on page 339, del Hoyo and Motis state that, “. . . only one sighting involved a group of nine birds (Brooks 1997b).” When one checks the cited reference however, flocks of nine were actually observed more than once.

Another criticism of this book is that it is not bilingual. Only one species of Cracid (the Plain Chachalaca, *Ortalis vetula*) occurs in the United States (in the southern-most three counties of Texas), whereas the other 49 species occur entirely in Latin America. As such, the primary audience of this book will be Latinos, whose first language may not be English. The hefty price of \$75.00 will also make this book prohibitive in the libraries where it is needed most. However, many of the cracidologists using this book will already

have web access to CSG’s trilingual publications and will be able to read there the material summarized in the del Hoyo and Motis chapter.—DANIEL M. BROOKS, Houston Museum of Natural Science, Houston, Texas; e-mail: dbrooks@hmns.org

**BIRDS OF THE BAJA CALIFORNIA PENINSULA: STATUS, DISTRIBUTION, AND TAXONOMY.** By Richard A. Erickson and Steve N. G. Howell (Eds.). American Birding Association Monographs in Field Ornithology No. 3, Colorado Springs, Colorado. 2001: 261 pp. ISBN: 1878788396. \$39.95 (paper).—This volume is a collection of eight papers and five appendices on the status and distribution of the birds of Baja California. In the preface, the editors lament the end of an era of “frontier” birding in Baja California—brought on by the publication of this volume. While discoveries of new species are certain to decline with time, I suspect that interest in birding and ornithology in Baja California will be enhanced by the information contained in this book. Perhaps the “frontier” era that Erickson and Howell lament the end of is the unbirded, wide open spaces and the chance for making new discoveries.

Several of the papers included in this book discuss breeding birds of Baja California. The first is a summary of breeding records for the nine eco-regions of the peninsula, with endemic species and subspecies highlighted. It is depressing to see the number of extinct endemic taxa listed, although most are limited to Guadeloupe Island, which has been heavily impacted by introduced mammals. Each eco-region is briefly described and dominant habitat types are noted. Typical breeding species are listed for each eco-region, with notes on endemic taxa and selected subspecies. Finally, a table lists taxa (including selected subspecies groups) and their breeding status for each eco-region. Short papers on breeding records for selected areas include reports on breeding birds of the Cerro Prieto geothermal ponds in the Mexicali Valley and the Vizcaíno Desert; these records are incorporated in the Regional compilation but more detailed information on breeding status is provided in these short papers.

Information on year-round status of selected Regions is also provided; most noteworthy is an annotated checklist for the Colorado Desert. Two papers discuss important observations and discoveries of birds in Baja California Sur and a summary of noteworthy records from 1967 to 1971. A third documents more recent, noteworthy records and includes brief descriptions for some of the observations, allowing interested readers access to the original field notes. The emphasis in this paper is on migration, and counts are given for various excursions the authors have made to Baja California during migration periods. A final annotated checklist of the birds of Baja is an appropriate conclusion to the papers.

Color figures are collected in one section, and include a remarkable set of photographs of rare birds, field sketches, photographs of selected habitats and eco-regions, and maps. The photographs are variable in quality, as one might expect of documentations of rare birds, but they represent a wonderful compi-

lation of the rare and noteworthy birds of Baja California.

Five Appendices are included as well. These consist of a database of selected observations, a list of notable specimens, a log of sight records archived at the San Diego Museum of Natural History, records of native species offered for sale or held in captivity (potential escapees), and a summary of species of potential conservation concern.

This monograph represents a wealth of information on the birds of Baja California. Although records of breeding or occurrence that are not accepted by the authors are not readily found in text, the book stands as a testament to the value of gathering information from a wide variety of sources and compiling it into a useful summary. This book is recommended to anyone with an interest in the status and distribution of birds.—MARY GUSTAFSON, USGS Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: mary\_gustafson@usgs.gov

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## THE WILSON BULLETIN

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FRONTISPIECE. Henslow's Sparrow (*Ammodramus henslowii*) in longleaf pine savanna in winter. Bechtoldt and Stouffer found an overall pattern of decreasing abundance with increasing time since burn treatment; seed abundance was the best predictor of Henslow's Sparrow relative abundance. Original painting (acrylic and gouache) by Barry Kent MacKay.

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## HOME-RANGE SIZE, RESPONSE TO FIRE, AND HABITAT PREFERENCES OF WINTERING HENSLOW'S SPARROWS

CATHERINE L. BECHTOLDT<sup>1,2</sup> AND PHILIP C. STOUFFER<sup>1,3,4</sup>

**ABSTRACT.**—Henslow's Sparrow (*Ammodramus henslowii*) is a declining, disturbance-dependent grassland bird that winters in the longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States. During two winters (2001, 2002), we estimated the relative abundances, movement patterns, and habitat associations of Henslow's Sparrows wintering in habitat patches differing in time since last burn (burn treatment). We conducted our study in southeastern Louisiana in *Andropogon* spp.-dominated longleaf pine savanna habitat. Henslow's Sparrows were most abundant in savannas burned the previous growing season, with a mean relative abundance of 2.6 individuals/ha. The most dramatic decline occurred between burn year 0 and year 1 (first and second winters after burning), when mean relative abundance dropped to 1.0 individual/ha. Home-range size of radio-tagged birds was not correlated with burn treatment. All radio-tagged individuals maintained stable home ranges, with a mean size of 0.30 ha. Vegetation characteristics differed significantly among burn treatments. Sites burned the previous growing season had low vegetation density near the ground, vegetation taller than 1.0 m, and high seed abundance. These variables were all highly correlated with Henslow's Sparrow relative abundance, but seed density best predicted Henslow's Sparrow numbers. We recommend a biennial, rotational burn regime to maintain habitat characteristics correlated with Henslow's Sparrow abundance. Received 8 November 2004, accepted 11 June 2005.

The Henslow's Sparrow (*Ammodramus henslowii*) is one of the fastest-declining disturbance-dependent bird species in North America. Breeding populations, which range from southern Canada through the Northeast and Midwest of the United States, have been decreasing at a rate of 8.6% per year since 1966 (Sauer et al. 2004), likely due to habitat loss (Askins 1993, Pruitt 1996, Herkert 1997, Cully and Michaels 2000). Breeding habitat requirements are generally well understood.

Henslow's Sparrows respond favorably to burning, haying, mowing, and hardwood reduction, achieving highest breeding densities 2–4 years after disturbance, when herbaceous vegetation is dense and woody vegetation is sparse (Zimmerman 1988; Herkert 1991, 1994, 1998; Swengel 1996; Herkert and Glass 1999; Cully and Michaels 2000).

Secretive winter behavior prevents an accurate regional estimation of winter population status, but there is some information on habitat use patterns. Henslow's Sparrows winter along the southeastern Gulf Coastal Plain, a region historically dominated by the fire-maintained longleaf pine (*Pinus palustris*) ecosystem. Studies in Mississippi (Chandler and Woodrey 1995), western Louisiana (Carrie et al. 2002), and along the Florida-Alabama border (Plentovich et al. 1999, Tucker and Robinson 2003) have revealed greater winter abundance of Henslow's Sparrows in

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recently burned or disturbed sites; furthermore, there is evidence that Henslow's Sparrows exhibit site fidelity over the winter, although no between-year recaptures have been documented (Plentovich et al. 1998). Home-range size during winter has not been estimated. Two studies have included banding wintering Henslow's Sparrows, but neither study has attempted to systematically estimate abundance using capture data (Chandler and Woodrey 1995, Plentovich et al. 1998).

Wintering Henslow's Sparrows have been associated with a variety of habitat characteristics, partially because each study conducted so far has considered a different community within the longleaf pine ecosystem. Habitat associations have been studied in lowland pitcher plant bogs, clearcut pine plantations, and upland savannas managed for timber production (Plentovich et al. 1998, 1999; Carrie et al. 2002; Tucker and Robinson 2003). Henslow's Sparrow presence and abundance have been correlated with the density of *Panicum verrucosum* and *Sarracenia* spp. (Plentovich et al. 1999), low litter depth and a high percent cover of herbaceous vegetation (Carrie et al. 2002), and high seed abundance and forb density (Tucker and Robinson 2003). No study has included dominant grass species composition among the vegetation measurements. Also, no study has emphasized winter habitat use of Henslow's Sparrows on upland longleaf pine savannas managed to restore the floristics of the savannas that historically dominated the southeastern Gulf Coastal Plain.

The longleaf pine ecosystem, including upland savanna communities, once dominated 25–36 million ha of the southeastern United States (Platt et al. 1988, Frost 1993, Stout and Marion 1993, Ware et al. 1993). Historically, fires occurred approximately every 1–3 years, usually during the summer (Frost et al. 1986, Stout and Marion 1993, Frost 1998). Longleaf pine savanna has a bi-layered habitat structure. Sparse stands of fire-tolerant longleaf pines form the overstory and a diverse herbaceous community occupies the understory. Without frequent fires, this ecosystem develops into a beech-magnolia-sweet gum forest (Ware et al. 1993).

In the Southeast, more than 98% of the original longleaf pine ecosystem has been lost

(Frost 1993, Ware et al. 1993, Noss et al. 1995). In Louisiana, 95–99% of this habitat has been destroyed (Noss et al. 1995). The remaining habitat consists of remnants scattered across the landscape, and it is estimated that less than 0.7% (280,000 ha) of that is in good, fire-managed condition (Frost 1993).

Considering the population declines and habitat loss experienced by Henslow's Sparrows, effective habitat management is vital. To assess the effects of prescribed burning on wintering Henslow's Sparrows in southeastern Louisiana, we intensively monitored savanna remnants managed under differing fire-return intervals. We used capture data to estimate relative abundance and radio-transmitters to provide the first estimates of home-range size for wintering Henslow's Sparrows; we report the first between-year recaptures of wintering individuals. We also conducted comprehensive measurements of habitat characteristics, including vegetation structure, species composition of grasses, and seed abundance. Finally, we discuss our results and make management recommendations based on our results and those of previous studies.

## METHODS

*Study sites.*—We chose eight study sites (see Table 1 for site names) located in St. Tammany and Tangipahoa parishes of southeastern Louisiana. This region lies on the boundary of the Coastal Plain Rolling Hills and Coastal Flatlands, historically dominated by longleaf pine/*Andropogon* spp. savanna (Frost 1993, Peet and Allard 1993). Study sites were dominated by native vegetation and were located within larger management areas composed of savanna and mixed woodlands. Site selection was based on amount of contiguous savanna (>15 ha) and relative cover of woody vegetation. We required study sites with <30% shrub cover so as not to impede mist-net sampling (see below).

At the time of the study, all sites had been fire-managed for at least 4 years, under the responsibility of The Nature Conservancy of Louisiana, the Louisiana Department of Wildlife and Fisheries, or the Girl Scouts of America. Study sites (areas sampled) were 2.25–7.5 ha; most were  $\geq 6.25$  ha (Table 1). Total savanna area surrounding each site differed. Study sites within the same burn regime were

TABLE 1. Burn treatments and recent fire history of eight study sites in longleaf pine savanna sampled during winters 2001 and 2002, in Tangipahoa and St. Tammany parishes, southeastern Louisiana.

Site name	Management area (size in ha)	Years since burn 2001	Years since burn 2002	Burn season and year	Area sampled 2001 (ha)	Area sampled 2002 (ha)
RAM	Lake Ramsay Wildlife Management Area (489.7)	Not sampled	0	Summer 2001 <sup>a</sup>	—	5.18
GSC	Camp Whispering Pines (19.0)	Not sampled	0	May 2001	—	2.25
BU1	Abita Creek Flatwoods Preserve (321.3)	0	1	May 2000	4.76	6.13
BU3	Abita Creek Flatwoods Preserve (321.3)	0	1	May 2000	7.03	6.69
LRS	Lake Ramsay Wildlife Management Area (489.7)	1	2	May 1999	6.25	6.25
LRN	Lake Ramsay Wildlife Management Area (489.7)	1	2	May 1999	6.25	6.25
TNC	Lake Ramsay Wildlife Management Area (489.7)	2	3	July 1998	7.50	6.25
WMA	Lake Ramsay Wildlife Management Area (489.7)	2	3	August 1998	6.25	6.25

<sup>a</sup> Exact date unavailable from management area records.

separated by  $\geq 0.63$  km. In 2001, we monitored six sites, comprising two replicates each of three burn regimes (burn treatments): 0, 1, and 2 years since last burn. Year-0 sites were burned the growing season prior to sampling; for example, a site burned in May 2000 was sampled in January 2001. In 2002, we followed these six sites as they transitioned into the next burn treatment level and added two replicates in the year-0 burn treatment (Table 1).

*Relative abundance sampling.*—Relative abundance estimates of Henslow's Sparrows were based on systematic mist-net sampling of each study site. Sampling took place during two consecutive winter seasons: January through February 2001 (winter 2001) and late November 2001 through February 2002 (winter 2002). During winter 2001, we sampled each site twice, once in January and once in February. During winter 2002, each site was sampled four times: we repeated the January and February (2001) sampling protocol at each study site, and we took two more samples of a 2.25-ha subset within each site. Subsets were chosen consistently across all study sites to measure 150 m on a side, starting at the most accessible corner of the 6.25-ha plot. We deviated from this protocol at three sites in 2002 because of limited volunteers, inclement weather, and unscheduled burn events. At

site GSC, we conducted three 2.25-ha samples. We sampled site TNC three times—two 6.25-ha samples and one 2.25-ha sample. WMA was sampled twice—one 2.25-ha sample and one 5.0-ha sample. Overall, we completed 40 sampling events on our eight study sites over the two study seasons.

For mist-net sampling, we used a team of 4–10 people, spaced 3 m apart, moving systematically across the study site (M. S. Woodrey pers. comm.). The team maintained their spacing throughout the sampling event to ensure even coverage of the site. Each time an *Ammodramus* sparrow flushed, the team marked the spot where they were walking, marked the area where the sparrow emerged from the herbaceous layer ("flush-from" location), and quickly set up a 6.0  $\times$  2.5-m mist net near where the sparrow landed (capture location). The team then attempted to flush the sparrow into the net. All captured individuals were banded with a federal band (size 0A). A subset of Henslow's Sparrows was fitted with radio-transmitters (see *Henslow's Sparrow movement patterns* below). Birds with radio-transmitters were released at their "flush-from" location and birds without radio-transmitters were released at their capture location.

*Relative abundance analysis.*—Based on their similar behavior as they flushed from the grass, we also pursued Le Conte's Sparrows

(*Ammodramus leconteii*), which often could be distinguished from Henslow's Sparrows only after being flushed into the net. During some sampling events, we detected one or more *Ammodramus* sparrows that we were unable to capture or otherwise identify to species level. To estimate the relative abundance of each species across our study sites, we assumed that the relative proportion of identified *Ammodramus* sparrows reflected the real relative abundance of each species. For each sampling event, we assigned unidentified *Ammodramus* individuals to either Henslow's or Le Conte's based on the abundance of identified *Ammodramus* sparrows during that sampling event. In 2001, we had to adjust 75% of the samples; in 2002, when Le Conte's Sparrow abundance was much lower, this adjustment was seldom needed (28% of samples adjusted).

We estimated relative abundance (Henslow's Sparrows/ha) by dividing the number of birds detected during a sampling event by the area sampled during that event. We used a nested analysis of variance (ANOVA) model to evaluate differences in relative abundance across burn treatments and study sites. Time since burn (burn treatment) was the main effect, site was nested within burn treatment, and sampling event was the sampling unit. Since previous studies have revealed that more recently burned sites should have a greater abundance of Henslow's Sparrows, we used an *a priori* contrast to compare Henslow's Sparrow abundance in burn treatment year 0 with all other burn treatments. We also evaluated whether sampling-team size was related to abundance estimates by regressing rank transformed Henslow's Sparrow abundance for the 40 sampling events on sampling-team size.

*Henslow's Sparrow movement patterns.*—A subset of birds ( $n = 27$ ) captured during sampling events of winters 2001 and 2002 were fitted with radio-transmitters to determine movement patterns. We followed two or three individuals on each replicate of burn treatments 0 and 1 in 2001 and on burn treatments 0, 1, and 2 in 2002 ( $n = 5$  sites). Transmitters (model BD-2A; Holohil Systems, Carp, Ontario, Canada) weighing 0.70 g (5.38% of mean body weight) were attached with elastic leg-loop harnesses (Rappole and Tipton

1991). Projected battery life was 21 days. Individuals were located daily by triangulation using a three-element yagi antenna and a Wildlife Materials TRX-64S (Murphysboro, Illinois) receiver. A single observer conducted all triangulations used in analyses. Locations consisted of 2–3 bearings to minimize time between triangulations (mean = 2.4 bearings). Mean time between triangulations was 5.9 min (SE = 0.53). Individuals were rarely seen, and triangulations were made from at least 12 m (mean = 41.4 m, SE = 2.98) away to minimize observer effects on the behavior of radio-tagged birds.

*Telemetry data analysis.*—Home-range estimates were based on 9 to 26 locations per individual (mean = 15.9, SE = 0.96). We used the program Location of a Signal (Ecological Software Solutions 2000) to compute locations from compass bearing data. Locations were entered into ArcView (ESRI, Inc. 1999) as Cartesian coordinates and we used the Animal Movement extension (Hooze and Eichenlaub 1997) to determine home-range size. We used a bootstrap ( $n = 100$ , interval = 1, with replacement) of the minimum convex polygon estimate of 11 locations ( $n = 16$  individuals) to determine mean home-range size. The bootstrap of nine locations ( $n = 18$  individuals) was used to analyze home-range size differences across burn treatments, study sites, and study years using ANOVA. Home-range size estimates were natural-log transformed to meet assumptions of normality and homogeneity of variances.

We examined the bootstrapped minimum convex polygon home-range estimates available for each individual to decide how many locations to include in the analyses described above. After nine locations (the minimum for any individual), the empirical mean home-range size reached 74% (SE = 0.03) of the bootstrapped estimate. With 11 locations, the empirical mean reached 83% (SE = 0.03) of the bootstrapped estimate. Based on these results, our mean estimate of home-range size probably represents at least 83% of the actual home range for all of our individuals, with more accurate estimates for most individuals. Home-range size for wintering Henslow's Sparrows stabilized at an average of 21 locations during a study at the Mississippi Sandhill Crane National Wildlife Refuge (Thatcher

TABLE 2. Dominant grass species encountered on longleaf pine savanna study sites in southeastern Louisiana during winters 2001 and 2002, grouped by morphotypes used in analyses.

Dominant grass morphotypes	Species included
<i>Andropogon</i> spp./ <i>Schizachyrium scoparium</i>	<i>Andropogon mohrii</i> , <i>A. virginicus</i> , <i>A. gerardii</i> , <i>Schizachyrium scoparium</i>
<i>Panicum virgatum</i> / <i>P. rigidulum</i>	<i>Panicum virgatum</i> , <i>P. rigidulum</i>
<i>Dichanthelium scabriusculum</i> , <i>Schizachyrium tenerum</i>	<i>Dichanthelium scabriusculum</i> , <i>Schizachyrium tenerum</i>
<i>Muhlenbergia expansa</i>	<i>Muhlenbergia expansa</i> (with mature inflorescences)
<i>Muhlenbergia expansa</i> (without mature inflorescences)	<i>Muhlenbergia expansa</i> (without mature inflorescences)
<i>Ctenium aromaticum</i>	<i>Ctenium aromaticum</i>
<i>Aristida</i> spp.	<i>Aristida purpurascens</i> , <i>A. dichotoma</i> , <i>A. affinis</i> , <i>A. palustris</i>
<i>Dichanthelium</i> spp.	<i>Dichanthelium longiligulatum</i> , <i>D. acuminatum</i> , <i>D. dichotomum</i>

2003), suggesting that our estimates were probably close to stabilizing for most birds.

We used regression analysis to look for relationships between the relative abundance and mean home-range size of Henslow's Sparrows at each site (bootstrap of nine locations,  $n = 21$  individuals). Mean relative abundance at each study site was determined by summing the number of Henslow's Sparrows/ha detected during each sampling event and dividing that number by the total number of sampling events at that site.

**Characterizing vegetation.**—During the two winter study seasons, we randomly chose ten 10-m-radius plots within each study site and sampled vegetation structure, dominant grass species composition, and seed abundance. The aggregate of plots covered 5% of the area at each study site. Only five vegetation plots were sampled at one study site (GSC), which was only 2.25 ha in area. The same observer conducted all vegetation sampling, always during February to early March, before the onset of spring growth.

We measured vegetation structure as vegetation height, type of tallest vegetation, and density (using a 2.0-m pole marked in 10-cm increments). We measured 21 points in each vegetation plot: the center point and 5 measurements (every 2 m) in each of the four cardinal directions (M. S. Woodrey pers. comm.). Vegetation height was measured as the tallest vegetation to fall within a 30-cm radius of the vegetation pole. We classified type of tallest vegetation as herbaceous or woody. Vegetation density was measured at 9 of the 21

points within each vegetation plot. We counted the number of vegetative contacts with the pole within each 10-cm increment to estimate density. Number of contacts ranged from 0 to 10; contact counts >10 were placed in the "ten" category. Percent cover of woody vegetation was measured by visually estimating (to the nearest 5%) shrub cover and by counting the number of trees >7.5 cm dbh within the plot.

In each plot, we visually estimated percent cover of dominant grass species to the nearest 5%. All herbaceous cover visible from above was included, so totals could be greater than 100% if a sparse layer of grasses or shrubs revealed an understory. In our estimates of percent cover, we grouped some species together if they had similar growth habits (Table 2). We separated one species, *Muhlenbergia expansa*, into plants with and without mature inflorescences. The mature inflorescences of *Muhlenbergia expansa* did not persist past the first winter, allowing us to readily distinguish plants that had flowered the previous growing season from those that had not.

We estimated relative seed abundance by counting the number of stalks with mature inflorescences within one randomly placed 1.0-m<sup>2</sup> frame in each vegetation plot. Stalks were identified to genus or to species level when possible. We removed the grasses *Dichanthelium* spp. and *Schizachyrium tenerum* from the seed abundance analysis because of the difficulty in distinguishing senescent stalks from seed-producing stalks of the season. We excluded one site (LRS 2001) in seed abun-

dance analyses because stalks with mature inflorescences were not identified to species during data collection.

*Vegetation analysis.*—Due to an unscheduled burn of one site, we collected vegetation data at only one site in the 3-year treatment. Therefore, we included only sites in the 0-, 1-, and 2-year treatments in the vegetation analysis, yielding four replicates of these three treatments over the study period.

We used two principal components analyses (PCA) with varimax rotation to describe vegetation structure and species composition of grasses across burn treatments and study sites. The PCA describing vegetation structure included vegetation height, vegetation density at heights from 0 to 0.3 m, percent shrub cover, number of woody contacts, and number of trees. We included vegetation density only from 0 to 0.3 m because a preliminary ANOVA showed that vegetation density at heights above 0.3 m did not differ among burn treatments. The PCA describing species composition included the percent cover values for the nine dominant grass species. Variables that loaded across more than one axis, or that did not load on any axis, were removed from the PCAs and treated separately.

PCA scores for structure and species composition were rank-transformed to meet assumptions for parametric tests, and a nested ANOVA model was used to test for differences in vegetation characteristics among burn treatments and among sites within burn treatments. Burn treatment was the main effect, sites were nested within burn treatment, and vegetation plot was the sampling unit. When tests were significant, we used Bonferroni multiple comparisons to compare variation among individual treatments (Sokal and Rohlf 1995). Percent cover values of dominant grass species that did not load in the principle components analysis were rank-transformed and included in the backwards-stepwise multiple linear regression analysis described below. We used SYSTAT (SPSS, Inc. 2000) for all analyses. Data points were considered outliers and removed from analysis if Student *t*-values were  $>3.0$ .

Seed abundance estimates were square-root transformed to meet assumptions of normality and homoscedasticity. We used a nested ANOVA model to examine differences in seed

abundance across burn treatments and sites within treatments. We used a Bonferroni multiple comparison to examine relative differences among burn treatments.

We used backwards-stepwise multiple linear regression analysis to examine the relationship of vegetation characteristics to Henslow's Sparrow abundance. Variables were eliminated from analysis if they did not explain a significant amount of variation in Henslow's Sparrow abundance ( $P > 0.05$ ) or if they were highly collinear (tolerance  $> 0.10$ ).

## RESULTS

*Abundance in relation to burn treatment.*—We detected 226 *Ammodramus* sparrows on the study sites over both years: 100 in 2001 and 126 in 2002. Identified birds included 135 Henslow's Sparrows, 23 LeConte's Sparrows, and 1 Grasshopper Sparrow (*Ammodramus savannarum*) during 40 sampling events. Of these, 88 Henslow's Sparrows were banded. Henslow's Sparrow abundance averaged  $1.17 \pm 0.32$  individuals/ha, but was highly variable among study sites, ranging from 0 to 4.50 individuals/ha.

Henslow's Sparrow relative abundance was highest in the most recently burned sites (ANOVA,  $F_{3,10} = 3.61$ ,  $P = 0.053$ ; *a priori* contrast 0 [mean =  $2.61 \pm 0.40$ ] versus all other burn treatments [mean =  $0.75 \pm 0.14$ ],  $F_{1,10} = 10.49$ ,  $P = 0.009$ ; Fig. 1). Henslow's Sparrow abundance did not vary significantly between study years (winter 2001: mean =  $0.84 \pm 0.21$ ; winter 2002: mean =  $1.45 \pm 0.26$ ; ANOVA,  $F_{1,38} = 2.05$ ,  $P = 0.16$ ), but did vary across study sites within burn treatments 0 and 2 (ANOVA, burn treatment 0:  $F_{3,7} = 19.74$ ,  $P = 0.001$ ; burn treatment 1:  $F_{3,8} = 1.39$ ,  $P = 0.32$ ; burn treatment 2:  $F_{3,8} = 15.22$ ,  $P = 0.001$ ; burn treatment 3:  $F_{1,3} = 1.80$ ,  $P = 0.27$ ). Mean sampling-team size was  $6.6 \pm 0.23$  people. Sampling-team size was evenly distributed across burn treatments and showed no relationship to the number of Henslow's Sparrows detected/ha ( $F_{1,38} = 0.64$ ,  $P = 0.43$ ,  $R^2 = 0.02$ ).

*Home-range size and site fidelity.*—We banded 32 Henslow's Sparrows in 2001. Among the 58 individuals captured in 2002, 2 were recaptures from 2001. Both recaptures were found within the management area of

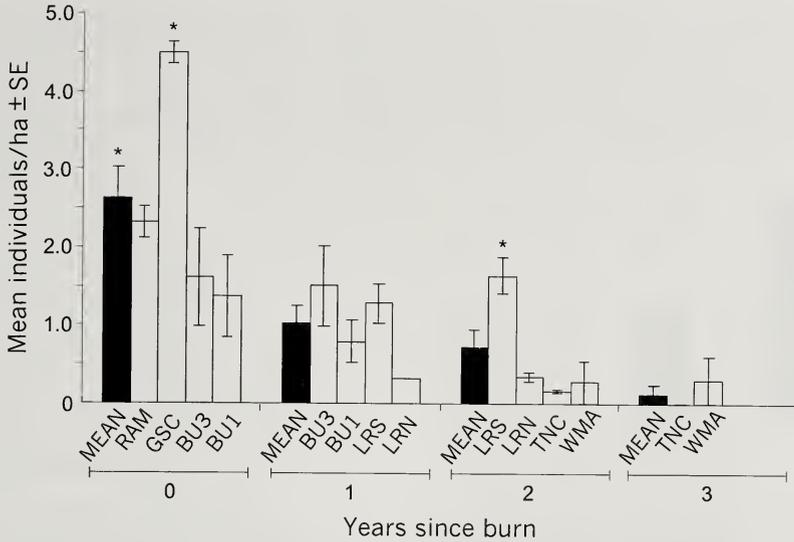


FIG. 1. In southeastern Louisiana during winters 2001 and 2002, Henslow's Sparrow abundance was greatest in longleaf pine savanna study sites the first winter after a burn, as revealed by a nested ANOVA and an *a priori* contrast of burn treatment 0 (i.e., 0 years since last burn) versus all other burn treatments (filled bars, significant difference indicated by asterisk). Mean abundance of Henslow's Sparrows varied within some burn treatments, but the overall pattern of decreasing abundance with increasing time since burn is apparent (unfilled bars). Asterisks over unfilled bars indicate significant differences within burn treatments, as revealed by one-way ANOVAs.

original capture; one was found on a different study site 1.6 km away (LRS burn treatment 1 to RAM burn treatment 0), and the other was found on the same study site (LRS burn treatment 1 to LRS burn treatment 2). We recaptured eight individuals within study years. Recaptures occurred in all burn treatments except year 3 and were always on the site of initial capture. The mean time between first and last capture was 42 days. Maximum time between captures was 70 days.

We radio-tagged 27 individuals at five study sites during winters 2001 and 2002. Of these, 21 individuals wore their radios long enough to allow estimation of home-range size ( $n = 9$  locations). Three individuals at LRN in 2001 were not included in calculations of mean home-range size or in analyses. Home-range sizes at LRN in 2001 ranged from 0.92 to 3.31 ha ( $n = 3$  individuals using 11 locations). These individuals were the only individuals monitored by a second observer and were outliers in all analyses. Including these outliers disproportionately influenced the mean home-range size estimate, but did not change the results of nonparametric tests of the analyses described below.

Home-range size varied from 0.09 to 1.50 ha ( $n = 16$  individuals using 11 locations). All radio-tagged individuals maintained stable home ranges over the sampling period. Mean home-range size for Henslow's Sparrows wintering on our study sites was 0.30 ha (SE = 0.09,  $n = 16$  individuals using 11 locations). Home-range size did not vary across study years ( $F_{1,16} = 0.30$ ,  $P = 0.59$ ) or sites ( $F_{4,13} = 0.97$ ,  $P = 0.46$ ; Fig. 2). There was no difference in home-range size across burn treatments ( $F_{2,15} = 0.52$ ,  $P = 0.61$ ). Home-range size was not related to relative abundance determined from mist netting ( $F_{1,6} = 2.13$ ,  $P = 0.20$ ,  $R^2 = 0.26$ ).

*Vegetation structure.*—The PCA of vegetation structure revealed two factors that explained 68.8% of the variation in the data. Mean density between 0 and 0.3 m and mean height were inversely related on principal components axis 1 (HEIGHT/DENSITY) and explained 43.0% of the variation. Number of trees, percent shrub cover, and number of woody contacts loaded positively on principle components axis 2 (WOODY) and explained 25.8% of the variation in the data. HEIGHT/DENSITY varied significantly among burn treat-

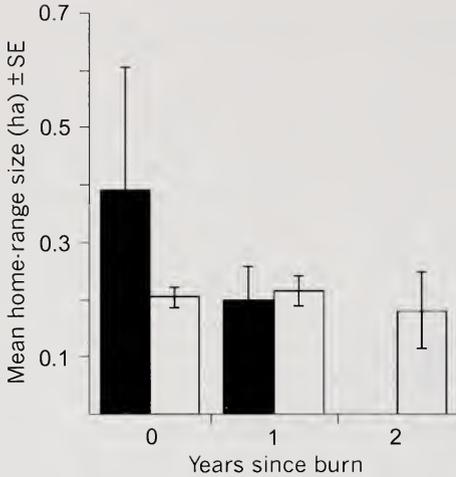


FIG. 2. Mean home-range size for Henslow's Sparrows ( $n = 18$  individuals, 9 locations) wintering in longleaf pine savannas of southeastern Louisiana during winters 2001 (filled bars) and 2002 (unfilled bars). Home-range size was not stable at nine locations, but our data showed that estimates at nine locations probably represented at least 74% of the actual home range for all individuals. Mean home-range size did not differ between study years, study sites, or burn treatments, as revealed by one-way ANOVAs.

ments ( $F_{2,9} = 24.32$ ,  $P < 0.001$ ; Fig. 3A). Year-0 sites had the lowest vegetation density close to the ground and the greatest vegetation height (Bonferroni, 0 versus 1,  $P = 0.007$ ; 0 versus 2,  $P < 0.001$ ; Table 3). Density increased and height decreased as time since burn increased. Individual study sites within burn treatment also differed from one another along the HEIGHT/DENSITY axis ( $F_{9,98} = 5.27$ ,  $P < 0.001$ ). The amount of woody vegetation did not differ among burn treatments ( $F_{2,9} = 0.91$ ,  $P = 0.44$ ; Table 3), although sites within burn treatment had significantly different amounts of woody vegetation ( $F_{9,98} = 3.98$ ,  $P < 0.001$ ; Fig. 3A).

*Grass species composition.*—Among the nine dominant grass morphotypes (Table 2), seven loaded onto two orthogonal factors, explaining 53.1% of the variation in the data set. Principal components axis one (SPECIES DIVERSITY) showed high positive loadings for *Dichantheium scabriusculum*, *Panicum virgatum*/*P. rigidulum*, and *Andropogon* spp./*Schizachyrium scoparium*. *Muhlenbergia expansa* without mature inflorescences and *Schizachyrium tenerum* had high negative loadings

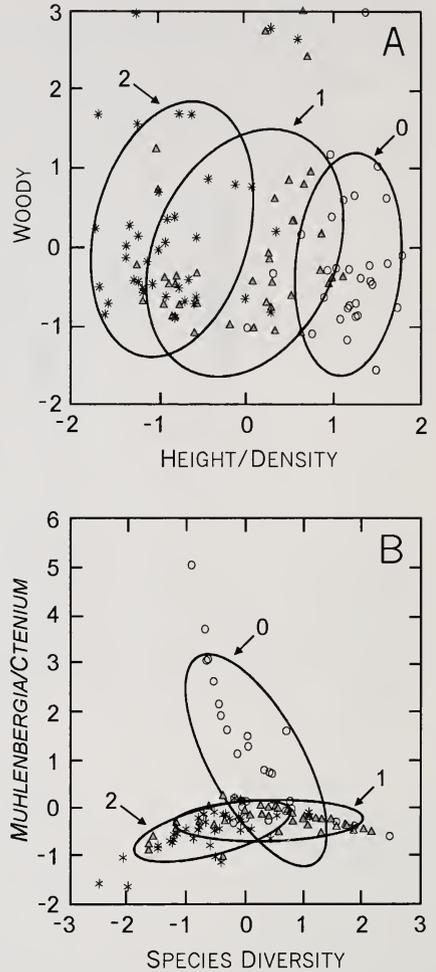


FIG. 3. Scatter plots of PCA scores for vegetation structure (A) and percent cover of dominant grass species (B) during winters 2001 and 2002 in southeastern Louisiana pine savannas. Each symbol represents a vegetation plot. Plots are grouped by burn treatment (0, 1, and 2 years since last burn), with ellipses delineating one standard deviation from the burn-treatment means. Circles represent plots in the year-0 burn treatment, triangles represent year 1, and asterisks represent year 2. (A) Burn treatments differ in height and density, but not in amount of woody vegetation. On the HEIGHT/DENSITY axis, year-0 sites had the tallest vegetation and the lowest vegetation density near the ground. On the WOODY axis, burn treatments did not differ in amount of woody vegetation. (B) Species diversity was slightly higher in the year-1 burn treatment than in the year-2 treatment. Sites in the year-0 burn treatment had significantly greater densities of *Muhlenbergia expansa* with mature inflorescences and *Ctenium aromaticum* than sites in the year-2 treatment.

TABLE 3. Mean vegetation measurements for southeastern Louisiana pine savannas in three burn treatment classes. Sites were either 0, 1, or 2 years since last burn, as sampled during the winters of 2001 and 2002. We used these variables, except seed abundance, which was considered separately, to create principal components factors representing vegetation structure and dominant grass species composition. Nested ANOVA revealed differences in vegetation structure, dominant grass species composition, and seed abundance among burn treatments.

Variable	Year 0		Year 1		Year 2	
	Mean	SE	Mean	SE	Mean	SE
Vegetation structure						
Height (m)	1.28	0.02	1.21	0.03	0.98	0.02
Density 0–0.1 m (no. of contacts)	3.31	0.24	6.55	0.31	8.08	0.28
Density 0.1–0.2 m (no. of contacts)	2.38	0.18	5.18	0.32	6.50	0.28
Density 0.2–0.3 m (no. of contacts)	1.37	0.15	2.95	0.23	3.88	0.18
Number of trees >7.5 cm dbh	1.93	0.41	2.00	0.53	2.39	0.58
Percent shrub cover	23.50	2.91	26.02	2.73	31.35	3.30
Number of woody hits	2.13	0.43	1.57	0.41	1.73	0.28
Percent cover of dominant grass species						
<i>Andropogon</i> spp./ <i>Schizachyrium scoparium</i>	21.33	2.47	16.50	2.07	18.00	2.39
<i>Panicum virgatum</i> /P. <i>rigidulum</i>	5.17	1.72	8.75	1.46	2.13	0.91
<i>Dichanthelium scabriusculum</i>	5.67	1.72	16.13	2.81	6.13	1.92
<i>Schizachyrium tenerum</i>	2.17	1.12	11.25	3.53	15.88	3.31
<i>Muhlenbergia expansa</i>	11.67	2.83	0.13	0.13	0.88	0.87
<i>Muhlenbergia expansa</i> (without mature inflorescences)	0.67	0.67	5.75	1.39	26.88	3.20
<i>Ctenium aromaticum</i>	8.67	3.06	0.00	0.00	0.00	0.00
<i>Aristida</i> spp.	3.17	1.00	6.88	1.35	11.13	2.61
<i>Dichanthelium</i> spp.	2.50	1.45	20.88	4.24	26.63	4.16
Seed density						
Number of stalks/m <sup>2</sup> with mature inflorescences	83.61	7.91	52.24	7.59	23.45	4.57

on this axis. High positive loadings indicate high species diversity and high negative loadings indicate low species diversity. Vegetation plots that load positively on this axis have a high proportion of a number of dominant species, while plots loading negatively are covered by just one or two dominant species. Principal components axis two (*MUHLENBERGIA/CTENIUM*) was characterized by high loadings of *Muhlenbergia expansa* with mature inflorescences and *Ctenium aromaticum* and explained 25.3% of the variation in the data. *Aristida* spp. and *Dichanthelium* spp. without mature inflorescences did not load onto either factor and are included separately in the multiple regression analysis described below.

Burn treatments were marginally distinct from one another along the SPECIES DIVERSITY axis ( $F_{2,9} = 3.20$ ,  $P = 0.10$ ; Fig. 3B). Year-2 sites loaded negatively on this axis and tended to be less diverse than sites in burn treatments 0 and 1. Year-2 sites were dominated by *Muhlenbergia expansa* with no mature inflorescences and/or *Schizachyrium tenerum* (Ta-

ble 3). Year-1 sites had positive loadings on this axis. These sites had high percent covers of *Dichanthelium scabriusculum*, *Panicum virgatum*/P. *rigidulum*, and *Andropogon* spp./*Schizachyrium scoparium* and tended to have the highest diversity of grasses (Table 3). Year-0 sites were better described by principle components axis two (*MUHLENBERGIA/CTENIUM*, see below). Sites within burn treatment levels differed significantly from one another along the SPECIES DIVERSITY axis ( $F_{9,97} = 6.78$ ,  $P < 0.001$ ).

The *MUHLENBERGIA/CTENIUM* principal components axis separated year-0 sites from year-2 sites ( $F_{2,9} = 5.70$ ,  $P = 0.025$ ; Bonferroni,  $P = 0.025$ ; Fig. 3B). Year-0 sites loaded high and positive on this axis and had a greater abundance of *Muhlenbergia expansa* with mature inflorescences and *Ctenium aromaticum* than year-2 sites (Table 3). Sites within burn treatment differed from one another in abundance of *Muhlenbergia* with mature inflorescences and *Ctenium* ( $F_{9,97} = 5.75$ ,  $P < 0.001$ ).

*Seed abundance.*—The number of stalks

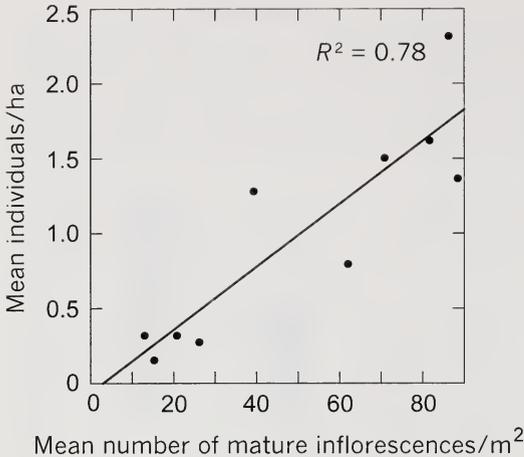


FIG. 4. Mean number of mature inflorescences/m<sup>2</sup> is the best predictor of Henslow's Sparrow abundance in southeastern Louisiana pine savannas during winters 2001 and 2002, as revealed by a backwards-stepping multiple linear regression relating habitat characteristics to Henslow's Sparrow abundance.

with mature inflorescences differed among burn treatments ( $F_{2,8} = 13.91$ ,  $P = 0.002$ ; Table 3). Seeds were more abundant at year-0 and year-1 sites than at year-2 sites (Bonferroni, 0 versus 1:  $P = 0.17$ ; 0 versus 2:  $P = 0.002$ ; 1 versus 2:  $P = 0.061$ ; Table 3). Seed abundance also varied among study sites within burn treatment ( $F_{8,86} = 2.15$ ,  $P = 0.039$ ), but it did not vary across study years ( $F_{1,105} = 0.82$ ,  $P = 0.37$ ). We removed three outliers with higher than expected seed abundances for their study site (Studentized residual  $> 7.0$ ).

*Relationship of Henslow's Sparrow abundance to vegetation characteristics.*—We used vegetation structure and species composition PCA scores, ranked percent cover values for *Aristida* spp. and *Dichantheium* spp., and values for seed abundance in a backwards-stepwise multiple regression analysis to examine the relationship between Henslow's Sparrow abundance and vegetation characteristics. Mean seed abundance was the best predictor of Henslow's Sparrow relative abundance ( $F_{1,8} = 27.74$ ,  $P = 0.001$ ,  $R^2 = 0.78$ ; Fig. 4). HEIGHT/DENSITY scores were significantly correlated with mean seed abundance values ( $r = 0.93$ ,  $P = 0.003$ ). HEIGHT/DENSITY scores were also highly, but not significantly, correlated with Henslow's Sparrow abundance ( $r =$

$0.78$ ,  $P = 0.20$ ). MUHLENBERGIA/CTENIUM, SPECIES DIVERSITY, and WOODY scores did not explain a significant amount of the variation in Henslow's Sparrow abundance, nor did the percent cover of two grass species that did not load onto the PCA, *Aristida* spp. and *Dichantheium* spp.

## DISCUSSION

The clear message from this and other studies is that Henslow's Sparrows use winter habitat with a recent history of disturbance. At our study sites, we saw the highest numbers of Henslow's Sparrows in longleaf pine savanna that was burned the previous growing season. Relative abundance of Henslow's Sparrows decreased with increasing time since burn. We found significant differences in relative abundance among individual study sites of the same burn age, but most sites changed predictably between years. Across sites, mean abundance decreased by over 90% between sites burned the previous growing season and those not burned for 3 years. Radio-tagged individuals maintained small, stable home ranges over the study period, but home-range size was not related to abundance or burn treatment. We also found evidence of between-year site fidelity.

As in our study, studies of Henslow's Sparrows inhabiting lowland pitcher plant bogs and upland savanna managed for timber production revealed an inverse relationship between abundance and time since burn (Carrie et al. 2002, Tucker and Robinson 2003). Mechanical disturbance may have the same effect as burning, at least on some clearcut pine plantations (Plentovich et al. 1999). It is unknown to what extent Henslow's Sparrows use other grasslands that experience periodic burning or mowing, such as power line right-of-ways and agricultural grasslands. Preliminary investigations have found Henslow's Sparrows wintering along power line right-of-ways (Burhans 2002; CLB unpubl. data). The restricted movement patterns of wintering Henslow's Sparrows may allow them to exploit these long, thin strips of habitat. Winter use of agricultural lands needs to be investigated, but land-use practices, such as midwinter haying, may have a negative effect on winter populations.

We used a novel mist-net sampling tech-

nique that proved to be an effective means of capturing, banding, and estimating the abundance of Henslow's Sparrows. We evaluated the technique by observing the behavior of 10 radio-tagged individuals during sampling events. All radio-tagged birds flew above and landed back into the herbaceous layer when approached by the sampling team, suggesting that individuals exhibit a predictable response when approached. There was no relationship between team size and relative abundance of Henslow's Sparrows, suggesting that variations in team size did not affect abundance estimates. Within seasons, we expected to recapture more than 8 of the 88 individuals banded; this low recapture rate suggests that individuals may learn net avoidance in subsequent sampling periods. We do not know whether differences in detectability among treatments may have influenced our results, but this could be examined with additional recapture data.

Our recapture and telemetry data confirm that Henslow's Sparrows exhibit within-season site fidelity (see also Plentovich et al. 1998). All within-year recaptures occurred within the 6.25-ha site of original capture, and recapture data showed that Henslow's Sparrows could use the same habitat patch for up to 70 days. Two individuals were recaptured between study years. Both recaptures occurred within the management area of original capture, including one within the same study site, which could suggest some local between-year site fidelity for wintering Henslow's Sparrows. The individual that returned to the same study site returned as the site transitioned to a year-2 burn treatment. This site (LRS) had a higher relative abundance of Henslow's Sparrows than any other site in the year-2 burn treatment, suggesting that this site was somehow more suitable for wintering Henslow's Sparrows, independent of burn treatment. The other returning individual exhibited a habitat use pattern predicted by our sampling results, moving from a site in burn treatment 1 (LRS), to a site 1.16 km away, burned the previous growing season (RAM). Plentovich et al. (1998) found that Henslow's Sparrows exhibited site fidelity over one season and speculated that the absence of between-year recaptures indicated that preferred winter site conditions were too ephemeral—compared to an

individual's life span—to encourage between-year site fidelity. While this seems likely, our two between-year recaptures indicated that some, possibly regional, form of between-year site fidelity may exist and that, depending on local conditions, habitat patches may remain suitable in consecutive seasons. Still, radio-tracking data and within-year recaptures suggest that arriving individuals must be able to select a habitat patch that will be suitable for the entire season. Examining settlement patterns and age-structure of wintering Henslow's Sparrows across a range of habitat patches may reveal more about how this process occurs.

Radio-tagged Henslow's Sparrows maintained stable home ranges over the winter. Radio-tagged individuals were consistently located in the same area of a study site over the sampling period. Our estimates of home-range size must be considered minimum estimates, as home-range size did not stabilize for any radio-tagged individual over the sampling period. Even so, our home-range size estimate (0.30 ha) roughly agrees with a simultaneous study of wintering Henslow's Sparrows at the Mississippi Sandhill Crane Refuge. In Mississippi, the mean home-range size (minimum convex polygon, 95% kernel) was 0.45 ha ( $n = 42$  individuals with at least 21 locations; Thatcher 2003).

Home-range size did not differ among burn treatments or across study years. Furthermore, home-range size did not show any relationship to relative abundance, a surprising observation, considering that home-range/abundance relationships are widely documented in the literature (Wiens 1973, Smith and Shugart 1987, Wunderle 1995, Haggerty 1998, Brown et al. 2000). Perhaps Henslow's Sparrows have partially overlapping, non-defended home ranges during winter, since abundance relationships usually occur when species maintain exclusive territories. Other investigators of wintering *Ammodramus* sparrows have observed a distinctive pattern of use of space in these species (Gryzbowski 1983, Gordon 2000). Small, weak-flying species with cryptic coloration are often solitary and evenly distributed across their habitat during winter (Pulliam and Mills 1977, Gryzbowski 1983). Gryzbowski (1983) suggested that this behavior may allow solitary species to exploit areas with less abun-

dant seed resources. These species' predator avoidance and resource acquisition strategies differ from those of gregarious, flocking species, which exhibit large-scale movements to exploit patches of resource-rich habitat (Grzybowski 1983, Gordon 2000).

It has been suggested that wintering Henslow's Sparrows may not require the large areas of grassland habitat essential to breeding populations (Herkert 1991, Burhans 2002). In lowland pitcher plant bogs, Tucker and Robinson (2003) found Henslow's Sparrows wintering in habitat patches as small as 0.06 ha. We did not test for the effects of area, but the differences in mean size of study sites among studies of wintering Henslow's Sparrows may be revealing. Our study sites were considerably larger than the majority of sites in previous studies (mean = 5.9 ha versus 0.2–1.0 ha) and all of our study sites were located within a larger matrix of savanna that had been burned within the last several years. Whereas Tucker and Robinson (2003) found that abundance of wintering Henslow's Sparrows increased with area, density was not related to bog area. This result could indicate that Henslow's Sparrows will use suitable habitat patches of any size, or it could reflect the fact that the majority of patches examined were very small (only 2 of 47 sites were >1.0 ha). Further investigations of settlement patterns and individual home-range overlap could shed more light on winter area requirements.

As in previous studies, we found that habitat characteristics varied across burn treatments and certain characteristics were correlated with relative abundance of Henslow's Sparrows. Vegetation structure, dominant grass species composition, and seed abundance varied across burn treatments. Sites burned the previous growing season had lower vegetation density within 0.3 m of the ground and greater vegetation height than sites burned 1 or 2 years prior to the previous growing season. Sites burned the previous growing season also had higher percent cover of *Muhlenbergia expansa* and *Ctenium aromaticum* and higher seed abundance than sites burned 2 years prior to the previous growing season. Sites burned 1 year before sampling had the highest species diversity of dominant grasses. We were surprised that the amount of woody vegetation did not vary across burn treat-

ments, but this could be a reflection of our site-selection criterion of minimal shrub cover.

Seed abundance stood out as the best predictor of Henslow's Sparrow relative abundance. A high percent frequency of seeds was also one of the most important predictors of Henslow's Sparrow occupancy of pitcher plant bogs along the Alabama/Florida border (Tucker and Robinson 2003). Similarly, on clearcut pine plantations in Alabama, one of the best predictors was the presence of *Panicum verrucosum* (Plentovich et al. 1999), a prolific seed producer that is common after soil disturbance. Like other *Ammodramus* species, Henslow's Sparrows probably rely mostly on seeds for their winter diet (Grzybowski 1983; M. S. Woodrey unpubl. data), although which seed species play the most important role in winter diet is unknown. Preliminary data indicate that *Muhlenbergia expansa*, *Dichanthelium* spp., *Rhynchospora* spp., and *Eupatorium* spp. may be important elements in the winter diet of Henslow's Sparrows (J. K. DiMiceli pers. comm.). Future studies should avoid overlooking inconspicuous species that could be important seed resources. For example, *Rhynchospora* spp. are a suite of species with diverse growth habits; some *Rhynchospora* produce tiny seeds and grow only a few centimeters tall. We observed these species forming a layer under taller grasses on some of our study sites, but did not include them in our measurements of species composition or seed abundance. These preliminary observations stress the importance of considering seed abundance and species composition at a fine scale.

After seed abundance, vegetation structure was the next most important predictor of Henslow's Sparrow abundance. Sites with vegetation heights >1.0 m and low vegetation density <0.3 m consistently had the greatest numbers of wintering Henslow's Sparrows. Carrie et al. (2002) also found that herbaceous cover and low vegetation density near the ground were important factors in discriminating between occupied and unoccupied sites. Tall vegetation may impede detection by predators, whereas low vegetation density near the ground may facilitate foraging movements for this weak-flying species.

Our habitat association results are supported by previous studies, although direct com-

parisons can be problematic. In two of the three previous studies, the second most important predictor of Henslow's Sparrow presence was high vegetation density at or below 1.0 m (Plentovich et al. 1999, Tucker and Robinson 2003); in our study, Henslow's Sparrow abundance was correlated with what is seemingly the exact opposite, low vegetation density near the ground. This apparent contradiction could have two sources. First, the relative difference in vegetation structure among our study sites is probably lower than in previous studies. We studied eight sites, located within continuous savanna habitat and dominated by native herbaceous species; the majority of our study sites were occupied by Henslow's Sparrows. Other studies examined a greater number of study sites representing a broader range of habitat structures and birds were absent from many of these sites. Second, the manner in which some studies quantified vegetation structure makes it difficult to separate vegetation density from vegetation height. In those studies, vegetation density was measured as the number of 10-cm increments where a certain type of vegetation was present (Plentovich et al. 1999, Tucker and Robinson 2003). Using this measure, sites with high vegetation density will also have taller vegetation, while not necessarily having high vegetation density near the ground. For example, on clearcut pine plantations (Plentovich et al. 1999) and lowland pitcher plant bogs (Tucker and Robinson 2003), Henslow's Sparrow presence/abundance was correlated with high densities of herbaceous cover. These results may correspond to our conclusion that abundance is greater on sites with taller vegetation, rather than contradict our vegetation density findings. Looking beyond these study-site and data-collection differences, studies of wintering Henslow's Sparrows seem to agree that tall vegetation, low vegetation density near the ground, and high seed abundance are positively correlated with presence or abundance of Henslow's Sparrows (Plentovich et al. 1999, Carrie et al. 2002, Tucker and Robinson 2003).

*Management implications.*—The absence of a natural disturbance regime on the southeastern Gulf Coastal Plain makes active management essential to wintering populations of Henslow's Sparrows. Habitat patches burned

the previous growing season, with vegetation >1.0-m tall, low vegetation density near the ground, and high seed abundance had the greatest relative abundance of Henslow's Sparrows across our study sites. Many herbaceous savanna species require a fire to flower, and species that follow fire often decrease in abundance as litter accumulates (Lemon 1949, Walker 1993). However, some herbaceous species are good competitors in the presence of litter, only reaching significant densities a few seasons after a burn, and fire interval may be important in maintaining seed bank diversity (Lemon 1949, Hodgkins 1958). Litter accumulation is also important in generating the high temperatures needed by some species to flower (Komarek 1965); burning too frequently can lead to a thin herbaceous layer, made up of a few fire-following species. Our relative abundance estimates demonstrate that a 10-ha area of savanna burned the previous growing season will support about 25 sparrows. After 1 year, the number will drop to around 10 individuals. Two years after a fire, the habitat will support approximately 1 individual/10 ha. If remnants of longleaf pine savanna and other similar grassland habitats are to support significant numbers of wintering Henslow's Sparrows, we recommend a biennial, rotating burn schedule. Future studies examining landscape-scale fire regimes, winter settlement patterns, predation risk, and diet are essential and will lead to a further refinement of these management recommendations.

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## SPACING AND PHYSICAL HABITAT SELECTION PATTERNS OF PEREGRINE FALCONS IN CENTRAL WEST GREENLAND

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**ABSTRACT.**—We examined nest-site spacing and selection of nesting cliffs by Peregrine Falcons (*Falco peregrinus*) in central West Greenland. Our sample included 67 nesting cliffs that were occupied at least once between 1972 and 1999 and 38 cliffs with no known history of Peregrine Falcon occupancy. We measured 29 eyrie, cliff, and topographical features at each occupied nesting cliff and unused cliff in 1998–1999 and used them to model the probability of peregrines occupying a cliff for a breeding attempt. Nearest-neighbor distance was significantly greater than both nearest-cliff distance and nearest-occupied distance (the distance between an occupied cliff and one occupied at least once, 1972–1999). Thus, spacing among occupied cliffs was probably the most important factor limiting nesting-cliff availability, and, ultimately, peregrine nesting densities. Although some unused cliffs were unavailable in a given year because of peregrine spacing behavior, physical characteristics apparently made some cliffs unsuitable, regardless of availability. We confirmed the importance of several features common to descriptions of peregrine nesting habitat and found that peregrines occupied tall nesting cliffs with open views. They chose nesting cliffs with eyrie ledges that provided a moderate degree of overhang protection and that were inaccessible to ground predators. Overall, we concluded that certain features of a cliff were important in determining its suitability as a nest site, but within a given breeding season there also must be sufficient spacing between neighboring falcon pairs. Our habitat model and information on spacing requirements may be applicable to other areas of Greenland and the Arctic, and can be used to test the generalities about features of Peregrine Falcon nesting cliffs throughout the species' widespread distribution. Received 31 March 2004, accepted 18 March 2005.

Habitat selection is the process by which an animal chooses suitable habitats (Manly et al. 1993, Litvaitis et al. 1994), and can be measured when an animal uses a resource disproportionately to its availability (Johnson 1980). Features of the habitat that are important for occupancy can function as meaningful indicators of habitat selection, even when the amount of available habitat is unknown (Manly et al. 1993). Historically, many researchers have studied Peregrine Falcons (*Falco peregrinus*; hereafter peregrine) in conjunction with the decline of populations caused by DDT in the mid-1900s (Cade et al. 1988), and there have been many descriptions of peregrine nesting habitat (e.g., White and Cade 1971, Court et al. 1987, Emison et al. 1997). However, there have been only two studies in

which there were quantitative tests of habitat features that influence habitat selection, and both studies occurred in temperate regions (Grebence and White 1989, Gainzarain et al. 2000). There are no such quantitative data for arctic environments, and there is little information on habitat characteristics that appear to be universal across the species' extensive distribution. Although Peregrine Falcons are described as intolerant of nesting pairs nearby (Cade 1960, Ratcliffe 1993), there have been no tests to evaluate the importance of spacing between suitable nesting cliffs or nearest neighbors. Gainzarain et al. (2000) calculated an average distance between nesting cliffs occupied by Peregrine Falcons, but this permitted only a general prediction of habitat use and was not a reflection of actual spacing. Availability of a nesting cliff may depend on the distribution of occupied nesting cliffs, which may vary among years (Ratcliffe 1993).

The two most important factors limiting raptor densities are the availability of physical nesting habitat or food, whichever is in shorter supply (Hickey 1942, Newton 1979). Newton (1998) suggested that nest-site availability can be limiting for species with specialized nesting-cliff requirements. Because peregrines

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prey opportunistically on many different bird species, the population trend of any one species usually does not affect peregrine breeding densities (Hickey 1942). In central West Greenland, most of the falcon's diet comprises four passerine species (Rosenfield et al. 1995); within 400 m of peregrine eyries, densities of these species are reduced, but they are abundant 400 to 3,000 m from the eyrie and at random locations on the study area tundra (Meese and Fuller 1989). Although peregrines may hunt regularly within 1,500 m of nesting cliffs (Tucker et al. 2000), some may travel 20–43 km on hunting flights (Enderson and Craig 1997). Newton (1998) suggested that food availability near nests is not important to species that forage elsewhere. Thus, nesting-cliff availability may be a more important limiting factor than local prey availability. Because of our limited knowledge of peregrine breeding biology in the Arctic and the importance of nesting-cliff availability, we investigated habitat selection and spacing as potential factors limiting peregrine nesting densities.

The migratory arctic Peregrine Falcon (Tundra Peregrine Falcon, *F. p. tundrius*) breeds in regions of Canada, Alaska, and the ice-free portion of Greenland (Cade et al. 1988, White et al. 2002). Since 1972, participants in the Greenland Peregrine Falcon Survey (GPFS) have routinely surveyed for breeding arctic peregrines in central West Greenland (Mattox and Seegar 1988). On the initial search, GPFS surveyors found only nine pairs of peregrines occupying cliffs. By 1999, there were 133 known peregrine nesting cliffs in the study area (W. G. Mattox unpubl. data). The 28 years of data collected on this population made it ideal for studying relationships between nesting-cliff occupancy, spacing, and physical habitat characteristics. Our objectives were (1) to determine whether availability of nesting cliffs was limited, (2) to evaluate whether unused cliffs were unsuitable or unavailable for occupancy because of peregrine spacing requirements, and (3) to determine which habitat characteristics may be important for peregrine nesting-cliff selection.

#### METHODS

*Study area.*—We conducted our study in the Kangerlussuaq region of central West Green-

land, which encompasses one of the widest portions of ice-free land on the island. The study area, delineated by W. G. Mattox and colleagues in 1972, is approximately 2,500 km<sup>2</sup> in area and lies between 66° 45' N and 67° 15' N (Mattox and Seegar 1988). Søndre Strømfjord—the longest fjord in West Greenland—divides the area, which extends approximately 100 km from the inland ice cap almost to the western coast. Elevations range from sea level to 1,120 m, and summer temperatures usually range between 0 and 15° C. Located in a belt of short, arctic vegetation, the landscape is dominated by willow scrub (*Salix glauca*), dwarf birch (*Betula nana*), lichens, mosses, sedges, and grasses (Böcher et al. 1968) interspersed with many ponds and lakes.

*Definitions.*—We defined an *eyrie* as the place on a ledge where a falcon lays her eggs (Ratcliffe 1993). We used the term *nesting cliff* to define a topographic feature containing one or more eyries or potential eyries, but occupied by only one pair of peregrines in a given year. Alternative nesting cliffs may occur within the range of one mated pair of birds. Rock faces and knolls were typically discrete topographic features in our study area and there was little continuous cliff habitat; thus, nesting cliffs were discrete features and did not overlap. *Availability* is the presence and accessibility of the habitat, or habitat feature, and is generally subject to the biological and social constraints of that species, which includes intra- and interspecific competition (Johnson 1980). Gyrfalcons (*F. rusticolus*) and Common Ravens (*Corvus corax*; hereafter ravens) were the only other common cliff-nesting species and only potential nest-site competitors. Gyrfalcons and ravens occupied nesting cliffs prior to the arrival of peregrines in the spring (W. G. Mattox pers. comm.), possibly influencing peregrine selection of nesting cliffs. Occupancy of nesting cliffs by Gyrfalcons varied widely among years and nesting cliffs (W. G. Mattox unpubl. data). In any year, Gyrfalcons and ravens combined occupied up to 8% of peregrine nesting cliffs and peregrines nested on up to 33% of nesting cliffs already occupied by either of these two species (W. G. Mattox unpubl. data). Therefore, the potential for interspecific competition for nesting cliffs was relatively low, and we

assumed that all nesting cliffs were available to peregrines at some time between 1972 and 1999. We classified a nesting cliff as *occupied* if we or other GPFS members observed a pair of peregrines at the nesting cliff during the breeding season (June–August) in any year from 1972 to 1999. The majority of these occupancies represented egg-laying attempts, but in a few cases adult pairs occupied nesting cliffs for several seasons without producing eggs (W. G. Mattox unpubl. data). We defined an *unused* cliff as any cliff where there was no known history or evidence of occupancy from 1972 to 1999. We considered only unused cliffs that had at least 14 m of vertical rock face because the shortest occupied cliff in the study area was 14 m in height. Our sample consisted of 105 cliffs; 67 were occupied and 38 were unused.

*Habitat measures.*—In the summers of 1998 and 1999, we measured nesting-cliff characteristics. Due to logistical constraints, we could not completely randomize our sample of nesting cliffs, but we measured all occupied and unused nesting cliffs encountered along or near portions of six survey routes established by the GPFS. Our sample of 105 cliffs constitutes approximately 50% of known cliffs in the study area, and the proportion of occupied to unused cliffs was likely representative of the total study area. Thus, despite a non-random sample, our estimate of nesting-cliff selection is meaningful, even when the standard error of features may not reflect the true variation in the total population of cliffs (Manly et al. 1993). For a complete description of GPFS survey methods, see Burnham and Mattox (1984).

We measured three features of nesting-cliff distribution by plotting all cliffs on a topographic map and measuring the linear distance between cliffs. The *nearest cliff* was the cliff closest to the sample cliff ( $n = 67$  occupied,  $n = 38$  unused), whether or not peregrines had ever occupied it. The *nearest occupied cliff* was the nearest nesting cliff occupied by peregrines at any time between 1972 and 1999. We measured the distance to the nearest cliff and the nearest occupied cliff from occupied and unused cliffs. We defined the third spatial measure, distance to *nearest neighbor*, as the distance to the nearest nesting cliff occupied by peregrines in the same breeding season as

the sampled nesting cliff. Because unused cliffs cannot have neighbors, we recorded this measure for occupied sites only. If the nearest-neighbor distance for a given nesting cliff varied among years, then we used the shortest distance recorded between 1972 and 1999.

We measured physical features of nesting cliffs at the three spatial levels: eyrie ledge, cliff, and surrounding topography. We measured 26 characteristics in addition to the three spacing features (Appendix) based on results from previous studies. A team of at least two persons hiked to cliffs and climbed to eyries and unused ledges to measure and record data. At occupied nesting cliffs, we measured the eyrie ledge used most recently. At unused nesting cliffs, we selected one ledge as a putative eyrie to measure. All measured ledges at unused nesting cliffs were flat ( $\sim 0^\circ$  slope) and at least large enough to accommodate a scrape for eggs. Although our selection of unused ledges was subjective, we attempted to select the ledge that provided the best combination of protection from predators and humans (Mearns and Newton 1988) and microclimatic benefits (Falk et al. 1986).

*Analyses.*—Because data deviated from normality, we used a nonparametric Wilcoxon matched-pairs signed rank test to compare among measures of spatial distribution for each occupied nesting cliff (Zar 1996). Comparisons between nearest-neighbor and nearest-cliff distances, and between nearest-neighbor and nearest-occupied cliff distances were not independent of one another, so we used a Bonferroni adjusted alpha of 0.025 to control for inflated type I errors.

To test for nonrandom orientation, we conducted Rayleigh's test of circular uniformity on aspect data for occupied and unused nesting cliffs (Zar 1996). Parametric tests for circular data assume the data are from a von Mises distribution, which is the circular equivalent to a normal distribution. As our data did not always meet the assumption for a parametric test, we used a nonparametric procedure for unimodal data that compared the mean direction of occupied and unused nesting cliffs against a chi-square distribution (Fisher 1993:116, Method P). This nonparametric procedure allowed us to evaluate whether or not cliff and eyrie ledge aspect

were important in peregrine nesting-cliff selection.

We used logistic regression to predict the probability of occupancy according to habitat features. Three habitat features—nearest-neighbor distance and cliff and ledge aspect—were not included in our logistic regression analysis because we could not calculate a value for unused cliffs (nearest neighbor) or the data were circular (aspect data) and could not be used appropriately in a linear analysis. Collinearity of predictor variables in linear or logistic regression can cause unexpected regression coefficients or large standard errors; thus, it was necessary to delete one or more intercorrelated variables before conducting our analysis (Hosmer and Lemeshow 1989, Zar 1996). We retained only one of a pair of correlated variables ( $r \geq 0.60$ ) that were easier to measure or that have been shown to be important features of peregrine nesting-cliff habitat elsewhere. We also eliminated one variable (slope) that we were unable to measure at all nesting cliffs. We eliminated 8 of 26 variables (eyrie height, cliff height at eyrie, elevation of cliff above the drainage, nearest cliff, elevation of cliff, length of ledge, overhang categories, and slope), retaining 18 for analysis.

With the 18 retained variables, we used the best subsets variable-selection technique to determine which variables to include in a logistic regression analysis and chose the combination of habitat variables that produced the best  $C(p)$  Mallows statistic (Hosmer and Lemeshow 1989). This technique provided all possible pairings among habitat variables and identified which combinations of variables provided the best fit to the data. We tested for the importance of interactions between certain habitat features in this variable selection step. Then, we used the combination of habitat variables identified as providing the best fit to the data in a logistic regression to predict the probability of occupancy (Hosmer and Lemeshow 1989, Allison 1999). We modeled the probability of each cliff being assigned to an occupied nesting cliff (1) as opposed to an unused cliff (0) based on habitat features. We evaluated the fit and the predictive power of the logistic regression model using the Hosmer-Lemeshow goodness-of-fit test ( $\hat{C}$ ) and the max-rescaled  $r$ -square value, respectively.

We used SAS software (SAS Institute, Inc. 1990) to conduct analyses and assigned a significance level of alpha equal to 0.05.

## RESULTS

The nearest-neighbor distance of 67 occupied sites was significantly greater than its paired, nearest-cliff distance ( $T_{0.05(2),67} = 333$ ,  $n = 67$ ,  $P < 0.001$ ). Nearest-neighbor distance was also significantly greater than its paired, nearest-occupied cliff distance ( $T_{0.05(2),67} = 52$ ,  $n = 67$ ,  $P < 0.001$ ).

We measured circular, linear, and categorical (Tables 1 and 2) habitat features at nesting cliffs that were occupied ( $n = 67$ ) and unused ( $n = 38$ ). Cliff aspect at occupied and unused nesting cliffs ( $Z_{0.05,67} = 26.25$ ,  $P < 0.001$ ;  $Z_{0.05,38} = 12.67$ ,  $P < 0.001$ , respectively) and on eyrie ledges or unused ledges ( $Z_{0.05,59} = 18.66$ ,  $P < 0.001$ ;  $Z_{0.05,34} = 10.24$ ,  $P < 0.001$ , respectively) was significantly oriented to the south. Mean orientation did not differ between occupied and unused cliffs ( $\chi^2 = 0.07$ ,  $n = 105$ ,  $P = 0.79$ ) or between used or unused ledges ( $\chi^2 = 0.28$ ,  $n = 93$ ,  $P = 0.60$ ).

The best subset variable-reduction technique identified five variables important in modeling nesting-cliff occupancy by peregrines (Table 3) and the slope of the logistic regression line was significantly different from zero ( $G_5 = 38.52$ ,  $n = 76$ ,  $P < 0.001$ ). Our logistic regression model was effective for describing occupied sites ( $\hat{C}_8 = 5.91$ ,  $P = 0.66$ ) and had moderate predictive power (rescaled  $r^2 = 0.54$ ). The adjusted odds ratio for each variable in the model indicates the effect of each variable on the probability of occupancy at a cliff. An odds ratio of 0.967 for vertical angle of exposure indicated that there is a 3.3% increase in odds of occupancy with every 1-degree decrease in exposure. Odds of occupancy increased by 89.3% if ledges were inaccessible to predators and by 96.7% if the ledge substrate was sand or dirt, rather than a stick nest. For every 1 m increase in cliff height and 1 m decrease in elevation of hill across valley, odds of occupancy increased by 1.7% and 0.7%, respectively.

## DISCUSSION

Spacing among occupied nesting cliffs was an important component of cliff occupancy in our study. Our results suggest that some near-

TABLE 1. Physical characteristics of 67 occupied and 38 unused cliffs measured to evaluate Peregrine Falcon nesting-cliff selection in central West Greenland. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.<sup>a</sup>

Physical features	Occupied			Unused		
	<i>n</i> <sup>b</sup>	Mean ± SE	Range	<i>n</i> <sup>b</sup>	Mean ± SE	Range
<b>Eyrie characteristics</b>						
Length of eyrie ledge (cm)	57	686.2 ± 152	50–6,089	28	234.7 ± 31.0	52–600
Depth of eyrie ledge (cm)	57	164.7 ± 32.7	17–1,500	28	105.4 ± 11.3	21–274
Eyrie aspect (°)	67	188.7 ± 0.9	15–345	34	195.1 ± 81.5	65–292
Horizontal angle of exposure (°)	49	144.4 ± 4.8	54–205	30	144.9 ± 8.4	65–236
Vertical angle of exposure (°)	48	65.2 ± 2.8	25–110	29	84.0 ± 6.4	20–150
<b>Cliff characteristics</b>						
Elevation of cliff (m)	67	288.0 ± 14.1	100–550	38	265.1 ± 20.1	75–550
Cliff height (m)	67	98.8 ± 8.0	14–365	38	61.0 ± 5.3	14–147
Height of hill below cliff (m)	67	39.8 ± 4.1	0–138	38	53.3 ± 7.7	0–198
Slope (m)	57	1.70 ± 0.11	0.71–5.08	32	1.34 ± 0.16	0.09–5.19
Cliff aspect (°)	67	187.7 ± 0.8	21–360	38	190.5 ± 1.3	20–330
Height of eyrie ledge (m)	65	51.1 ± 5.4	5–224	35	24.8 ± 3.2	7–78
Cliff height at eyrie ledge (m)	65	94.3 ± 8.2	14–365	35	52.2 ± 5.7	14–154
<b>Topographical characteristics</b>						
Distance to permanent water (m)	67	452.7 ± 55.4	0–2,750	38	561.3 ± 81.9	0–2,500
Elevation gain within 3-km radius (m)	67	205.2 ± 11.3	50–475	38	179.6 ± 14.4	25–500
Elevation of cliff above drainage (m)	67	161.4 ± 10.8	26–450	38	130.9 ± 11.5	25–300
Distance to drainage (m)	67	577.9 ± 72.4	0–2,250	38	643.8 ± 84.1	0–2,000
Elevation of hill across valley (m)	67	348.6 ± 14.0	125–600	38	399.4 ± 26.9	125–750
Distance to hill across valley (km)	67	2.19 ± 0.14	0.3–5.0	38	2.6 ± 0.2	0.5–6.5
Distance to nearest cliff (km)	67	2.16 ± 0.14	0.2–5.0	38	1.4 ± 0.1	0.2–3.3
Distance to nearest occupied cliff (km)	67	2.69 ± 0.13	0.3–5.1	38	2.1 ± 0.2	0.2–5.0
Distance to nearest neighbor (km)	67	3.27 ± 0.18	1.3–11.2		N/A	

<sup>a</sup> See Appendix for definition of habitat features.

<sup>b</sup> At a few nesting cliffs and unused cliffs, we were unable to access or could not identify the eyrie or unused ledge. Thus, our sample size for eyrie characteristics or location varies from 67 occupied nesting cliffs and 38 unused cliffs. We also could not calculate slope of cliff if we could not measure accurately the distance from the observer to the top of the cliff.

est nesting cliffs, occupied at least once and, thus, suitable, are not available in some years due to their proximity to a site already occupied by peregrines. Therefore, availability of a particular nest site may vary among years depending on the current distribution of occupied nesting cliffs. Dispersion among animal-use areas can result from a variety of causes, including competition for food or nesting resources (Fretwell and Lucas 1969, New-

ton 1998). Intraspecific aggression of peregrines has been noted at nest sites (Ratcliffe 1993, White et al. 2002), and spacing requirements may be a mechanism for reducing the costs associated with agonistic behavior.

Unused nesting cliffs also may not be available in every year because of peregrine spacing requirements. However, we can assume that unused cliffs were available for occupancy at some time between 1972 and 1999 be-

TABLE 2. Categorical habitat features measured at 67 occupied nesting cliffs and 38 cliffs unused by Peregrine Falcons to evaluate habitat selection in central West Greenland. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.<sup>a</sup>

Physical features	Occupied <sup>b</sup>	%	Unused <sup>b</sup>	%
<b>Ledge characteristics</b>				
Overhang protection on ledge				
None	6	11%	15	47%
Slight	10	18%	6	19%
Partial	29	54%	5	16%
Complete	9	17%	6	19%
Accessible to predation				
Yes	16	28%	15	47%
No	42	72%	17	53%
Substrate at or near scrape				
Sand or dirt	44	81%	11	38%
Moss	0	0%	3	10%
Vegetation	6	11%	9	31%
Gravel	1	2%	2	7%
Stick nest	2	4%	4	14%
Bare rock	1	2%	0	0%
Vegetation on ledge				
Yes	42	74%	22	65%
No	15	26%	12	35%
<b>Cliff characteristics</b>				
Vegetation at base of cliff				
Willow-steppe mix	21	33%	18	47%
Heath-willow mix	18	28%	14	37%
Heath-steppe mix	8	13%	3	8%
Herbslope	5	8%	0	0%
Water	4	6%	1	3%
Willow copse	8	13%	2	5%
Boulders at base of cliff				
Yes	57	89%	25	66%
No	7	11%	13	34%
Position of ledge on cliff				
Lower	15	24%	9	20%
Middle	30	48%	31	69%
Upper	18	29%	5	11%
Human disturbance				
Minimal	57	85%	33	87%
Moderate	9	13%	5	13%
Severe	1	1%	0	0%

<sup>a</sup> See Appendix for definition of terms.

<sup>b</sup> At a few nesting cliffs and unused cliffs, we were unable to access or could not identify the cyrie or unused ledge. Thus, our sample size for cyrie characteristics or placement varies from 67 occupied nesting cliffs and 38 unused cliffs.

cause no nesting cliff was occupied in each of the last 28 years (peregrines occupied nesting cliffs 20–96% of years checked after the nesting cliff was located), and breeding pairs moved up to 3.5 km among years to alternative nesting cliffs (W. G. Mattox unpubl. data). Spacing of cliffs was also not important

in our logistic regression model predicting nesting-cliff occupancy. Thus, some unused nesting cliffs are probably unsuitable regardless of their availability because they do not contain features important for peregrine nesting.

The cyrie ledge features that we identified

TABLE 3. Peregrine Falcons in central West Greenland selected tall nesting cliffs with prominent views and eyrie ledges that provided protection from weather and predators. Our logistic regression model predicts the probability of a cliff being occupied by peregrines using habitat features measured at 48 occupied nesting cliffs (1) and 28 unused cliffs (0). Negative coefficients ( $\beta$ ) indicate a negative association between that variable and cliff occupancy. Habitat variables included in our model were selected using the best subset variable-selection technique. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.<sup>a</sup>

Variable <sup>b</sup>	$\beta$	SE	Wald $\chi^2$	df	P <sup>c</sup>	exp( $\beta$ ) <sup>d</sup>	95% Wald	CL
Intercept	5.715	1.808	9.99	1	0.002	—	—	—
Vertical angle of exposure	-0.034	0.015	5.37	1	0.020	0.967	0.939	0.995
Accessibility of ledge	-2.239	0.765	8.56	1	0.003	0.107	0.024	0.478
Stick nest on ledge	-3.413	1.231	7.68	1	0.006	0.033	0.003	0.368
Cliff height	0.017	0.007	5.56	1	0.020	1.017	1.003	1.032
Elevation of hill across valley	-0.008	0.003	8.13	1	0.004	0.992	0.987	0.998

<sup>a</sup> We were unable to measure all eyrie and ledge characteristics at all cliffs because of accessibility problems. Our sample for the logistic regression model is lower than our complete sample of 67 occupied nesting cliffs and 38 unused cliffs because it includes only those cliffs where all five habitat variables were measured.

<sup>b</sup> See Appendix for definition of terms.

<sup>c</sup> P-values based on Wald  $\chi^2$  statistic.

<sup>d</sup> Odds ratios indicate the change in odds of occupancy for each unit change of the variable. For example, the odds ratio for elevation of hill across the valley is 0.992. This means that for each 1 m decrease in elevation the odds of occupancy increase by 0.8%. Accessibility of ledge and stick nest on ledge are binary variables; thus, the odds ratios reflect 89.3% and 96.7% increases in odds of occupancy, respectively, if the ledges are not accessible (by foxes or humans) or there is not a stick nest on the ledge.

as being important in nesting-cliff occupancy suggest that peregrines choose nesting sites with ledges that provide microclimatic benefits and protection from predators. Eyrie ledges that afford protection from weather are associated with occupancy by peregrines throughout North America (Cade 1960, Falk et al. 1986, Court et al. 1988). Bradley et al. (1997) found that mean clutch size of peregrines in subarctic Canada decreased with greater precipitation and that nestling mortality increased with annual precipitation during storms. This suggests that microclimate of the eyrie, influenced by vertical protection of the overhang above the ledge, may be an important feature in nesting-cliff occupancy by peregrines.

Approximately one-third of peregrine eyries in Great Britain were on raven stick nests (Ratcliffe 1993) and, in Alaska, 20% nested on Rough-legged Hawk (*Buteo lagopus*) stick nests (Cade 1960). Thus, stick nests can provide a suitable substrate for peregrine eyries. Ravens in our study area began nesting in early May and tended to build their stick nests under rock overhangs that completely shaded the ledge (CSW pers. obs.). The negative association we found between nesting-cliff occupancy and stick nests may represent selection for moderate, rather than complete, overhang protection on the ledge. Moderate over-

hang protection would provide some protection from weather, but also allow peregrines to receive warmth from the arctic sun. Most cliffs were oriented to the south and therefore were positioned to take advantage of solar insolation. Our results support those of Burnham and Mattox (1984), who suggested that peregrines in central West Greenland choose eyrie ledges that balance solar exploitation and protection from weather.

Peregrine nesting cliffs in several regions of the world are associated with tall, dominant cliffs that provide a commanding outlook (Hickey 1942, Grebence and White 1989, Gainzarain et al. 2000). Jenkins and Hockey (2001) proposed a latitudinal gradient in cliff height, suggesting that peregrines occupied low cliffs in arctic regions (mean cliff height <10 m at 65° latitude). Our data, however, indicate that peregrines will choose tall cliffs with commanding views, if available, in arctic areas, as well. Tall cliffs and open views apparently benefit peregrines by providing better perches for hunting or defense from intruders (Mearns and Newton 1988, Ratcliffe 1993, Jenkins 2000). Jenkins (2000) documented greater hunting success from perches at nesting cliffs than from aerial hunts, and he found a positive relationship between hunting success and tall cliffs. However, in our study area the primary prey of peregrines were ground

nesting and foraging passerines (Rosenfield et al. 1995), which suggests that the contour-hugging, surprise attack behavior described by White and Nelson (1991) may be a more effective strategy for capturing prey than aerial attacks from cliffs. Thus, the benefits of defense from conspecifics and predators (e.g., arctic fox, *Alopex lagopus*), rather than enhanced foraging opportunities provided by tall nesting cliffs with commanding views, are probably more influential in nesting-cliff selection. We conclude that competition plays an important role in nesting-cliff suitability, as well as availability.

We identified features that were limited in availability but important for nesting-cliff selection by peregrines. However, certain features important in habitat selection may be abundant in our study area and, therefore, our methods may not have allowed us to identify these features. For instance, Cade (1960), Ellis (1982), and Court et al. (1988) found that peregrine nesting cliffs often were close to water. Surface water provides a place for peregrines to bathe and good habitat for some of their prey (Cade 1960). However, we found no association between occupied nesting cliffs and distance to water. There is an abundance of small lakes and streams in our study area, so water is generally found close to all cliffs (mean = 492.0 m  $\pm$  46.2 SE, range = 0–2,750 m).

Of the many habitat features we measured, we found five that characterized occupancy by peregrines. Nesting cliffs may be suitable to peregrines by meeting just a few critical spatial and habitat requirements. This adaptability in nest-site selection may contribute to the worldwide distribution of peregrines. Spacing, and thus availability, of suitable breeding sites is probably the most important proximate factor limiting the nesting densities of peregrines in our study area. Characteristics of the nesting cliff are important for determining the suitability of a nesting cliff if there is sufficient space between neighbors to accommodate a breeding attempt in a given year. Our results suggest that peregrines select tall nesting cliffs with commanding views and protected ledges for nest-defense and microclimatic benefits. The similarities of nesting-cliff features at occupied peregrine nesting cliffs among geographic regions suggest that our

predictive model of nesting-cliff occupancy—using physical characteristics and peregrine spacing requirements—could be applicable to other areas of Greenland and the Arctic.

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APPENDIX. Description of physical characteristics measured at 67 occupied nesting cliffs and 38 cliffs unused by Peregrine Falcons in central West Greenland. Measurements were made in 1998–1999; cliffs were categorized as occupied or unused based on their occupancy history from 1972 to 1999.

Feature	Description	Method
<b>Cliff features<sup>a</sup></b>		
Elevation (m)	Meters above sea level at top of cliff	Topographic map
Cliff height (m)	Cliff height from base of cliff to highest point, not including any ledges or tiers	Rangefinder and clinometer <sup>b</sup>
Slope (m)	Slope of cliff calculated as rise/run	Rangefinder and clinometer <sup>c</sup>
Height of hill below cliff (m)	Measured from base of hill to bottom of cliff formation	Rangefinder and clinometer <sup>b</sup>
Aspect of cliff (°)	Aspect perpendicular to rock face	Compass
Vegetation	Predominant vegetation types below cliff face	Direct observation
Boulders	Presence of boulders at base of cliff	Direct observation
Height of ledge (m)	Height from base of cliff to ledge	Rangefinder and clinometer <sup>b</sup>
Height of cliff at ledge (m)	Cliff height intersecting ledge	Rangefinder and clinometer <sup>b</sup>
Position of ledge on cliff	Upper, center, lower and right, middle, left	Direct observation
Human disturbance	Minimal: >5 km from human settlement or roads Moderate: 1–5 km from human settlements or roads Severe: <1 km from human settlements or roads	Topographic map
<b>Ledge features<sup>d</sup></b>		
Ledge length (cm)	Length of ledge at longest point	Measuring tape
Ledge depth (cm)	Depth of ledge at widest point	Measuring tape
Aspect of ledge (°)	Aspect of ledge perpendicular to back wall	Compass
Horizontal angle of exposure (°)	Degree of opening to right and to left of ledge	Compass
Vertical angle of exposure (°)	Back wall of ledge to front lip of roof at ledge	Clinometer
Accessible by fox or human	Yes or no	Direct observation
Substrate material on ledge	Bare rock, gravel, sand/dirt, vegetation, or stick nest	Direct observation
Vegetation on ledge	Yes or no	Direct observation
Overhang protection on ledge	None: 0% of ledge shaded midday Slight: 1–25% of ledge shaded midday Partial: 50–75% of ledge shaded midday Complete: ledge completely shaded midday	Direct observation
<b>Topographical features</b>		
Total elevation gain (m)	Elevation of cliff minus lowest elevation within a 3-km radius circle around nesting cliff	Topographic map
Elevation above drainage (m)	Elevation of cliff minus elevation of drainage	Topographic map
Elevation of hill across valley (m)	Elevation of hills across valley from cliff	Topographic map
Distance to permanent water (m)	Distance from cliff to permanent water	Topographic map
Distance to drainage (m)	Distance from sample cliff to closest drainage	Topographic map
Distance to hills across valley (km)	Distance from cliff to hills across valley	Topographic map
Nearest cliff (km)	Distance from sample cliff to nearest cliff regardless of occupancy status	Topographic map

## APPENDIX. Continued.

Feature	Description	Method
Nearest occupied cliff (km)	Distance from sample cliff to nearest cliff occupied by peregrines at least once between 1972 and 1999	Historical data and topographic map
Nearest neighbor (km)	Distance from sample cliff to nearest cliff occupied in same year	Historical data and topographic map

<sup>a</sup> Continuous vertical rock >14 m tall surrounding the eyrie or putative eyrie.

<sup>b</sup> All cliffs were level with or higher than the observation point. Height was measured by calculating the height to the top and bottom of the cliff from the observation point (e.g., distance to top  $\times$  sin [angle to top]) and then subtracting the bottom height from the top height. For a few tall cliffs, we were unable to measure the distance to the top of the cliff. To measure height at these cliffs, we used the equation: height =  $a \times b$ , where  $a$  = the angle to bottom of cliff  $\times$  angle to top of cliff, and  $b$  = distance to bottom of cliff  $\times$  secant from observation point to bottom of cliff.

<sup>c</sup> Slope could not be calculated at those cliffs where we could not measure the distance to the top of the cliff because the horizontal distance of the cliff (run) was unknown at these sites.

<sup>d</sup> Place on ledge where eggs laid. On unused ledges, measures were taken from the best potential eyrie ledge (i.e., 0° slope).

## SURVIVAL AND CAUSES OF MORTALITY IN WINTERING SHARP-SHINNED HAWKS AND COOPER'S HAWKS

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**ABSTRACT.**—Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) are important predators of birds in North America, but little is known about their natural history during the winter. Even basic survival information is not well documented in these species and is generally unknown during the winter. Therefore, we examined survivorship and causes of mortality among wintering Cooper's and Sharp-shinned hawks. We radio-tracked 27 Cooper's and 40 Sharp-shinned hawks during 5 winters from 1999 to 2004. Neither species nor sex was a significant covariate of survivorship, but the probability of adult survival (75.4%) over 110 days was significantly higher than that of juveniles (9.4%). Our estimate of adult survivorship is comparable with those published for other accipiters, but our estimate for juveniles is lower. Age differences in survivorship may be attributed to risk taking or inexperience in juveniles and/or difficulties in dealing with transmitter attachments. Two types of mortality (predation and collisions) were observed in the study. Whereas predation by owls was a major source of mortality in rural habitat, no predation was observed in the urban habitat. Our results suggest that predation by owls may have important implications for the behavioral interactions between accipiters and their prey. Received 20 October 2004, accepted 31 May 2005.

Although Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) are the main predators of small birds wintering in North America, very little is known about their natural history during the winter. Even basic information, such as diet, hunting patterns, general movements, and home-range size, is lacking (Rosenfield and Bielefeldt 1993, Bildstein and Meyer 2000). This lack of information is particularly problematic given that these hawks play a critical role in an important conceptual paradigm in behavioral ecology: the small-bird-in-winter. Under this paradigm, small birds face trade-offs between the risks of starvation and predation from accipiter hawks. This conceptual paradigm has had great impact on our present understanding of many aspects of behavioral ecology, such as sociality (Pulliam and Caraco 1984, Boiniski and Garber 2000), foraging behavior (Lima 1985, Stephens and Krebs 1986), and predator-prey theory (Mangel and Clark 1988, Houston and McNamara 1999).

Like other aspects of their natural history, the demography of Sharp-shinned and Cooper's hawks is poorly understood (Rosenfield

and Bielefeldt 1993, Bildstein and Meyer 2000). Basic survivorship estimates and the relative importance of causes of mortality are unknown during winter and rarely documented during the rest of the year. Much of what we know about accipiter survival is based on banding data (see Keran 1981). For Cooper's Hawks, survivorship estimates from band recoveries are 19–28% for first-year birds and 63–79% for older birds (Henny and Wight 1972, Boal 1997). Some recent telemetry information from breeding studies of Cooper's Hawks in urban sites resulted in survivorship estimates of 49% for nestlings (Boal and Mannan 1999) and 67% from post-fledgling to midwinter (Mannan et al. 2004), but no other estimates of survivorship have been published for adults. Similarly, limited band recoveries published by Palmer (1988) resulted in survivorship estimates of 20–25% for Sharp-shinned Hawks. To our knowledge, there are no other published data on the survivorship of these two species.

Although relatively little information exists on Cooper's Hawks and Sharp-shinned Hawks, perhaps the best available insights into their survival rates come from studies of other accipiters. In North America, Northern Goshawk (*A. gentilis*) survivorship is estimated at 33% for first-year birds, 68% for sub-adults, and 81% for adults (Squires and Reynolds 1997). Dewey and Kennedy (2001) estimated a greater average first-year survivorship

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(control group only, 73%), similar to that estimated for sub-adults by Squires and Reynolds (1997). Another source of information on accipiter survivorship comes from European studies of the goshawk and the Eurasian Sparrowhawk (*A. nisus*). Tornberg and Colpaert (2001) estimated goshawk survivorship at 43% for first-year birds, and about 84% in older birds. Kenward et al. (1999) estimated similar rates of survival at approximately 50% for first-year males, 70% for first-year females, and about 80% for both sexes in older birds. While juvenile survivorship is considerably lower in sparrowhawks (30% for males, 50% for females) than in goshawks, adult survival rates are comparable at nearly 70% for both sexes of both species (Newton 1975; Newton et al. 1983, 1999). Based on the information available for other accipiters, the general pattern seems to be that juvenile survival is approximately half that of adults.

Little consideration has been given to the causes of mortality in post-fledgling Sharp-shinned and Cooper's hawks. Based on the scant information that exists, human-induced mortality seems to be due mainly to collisions with windows or automobiles (Keran 1981, Klem 1990, Klem et al. 2004) and electrocution (Lehman 2001). Similarly, Boal (1997) attributed 68% of adult Cooper's Hawk mortality to collisions with automobiles or windows, and 3% to electrocution. As urban populations of accipiters (especially Cooper's Hawk) increase, such "accidental" mortality may become increasingly common (see Boal and Mannan 1999). Mortality due to gunshot and poison (important causes of mortality in the past) have greatly diminished since implementation of federal protection and the elimination of DDT/DDE in North America (Keran 1981), although Boal (1997) reports recent mortality rates from gunshot (13%) and poison (6%) for Cooper's Hawks. Natural predation by owls and other raptors on accipiters has been documented (Klem et al. 1985, George 1989), but the demographic importance of such predation is unknown. Disease may also be an important mortality factor, particularly during the breeding season (Ward and Kennedy 1996, Boal et al. 1998).

The objective of our research was to obtain a better understanding of accipiter natural history and behavior, with the long-term goal of

obtaining insight into predator-prey interactions in wintering birds. We studied the behavior and general natural history of Cooper's and Sharp-shinned hawks over several winter periods. Here, we present data on one aspect of accipiter natural history: winter survival and causes of mortality. As little is known about North American accipiters, predictions are difficult; however, our expectation was that Sharp-shinned Hawks were more likely targets of predation due to their smaller size, which may result in lower survival relative to that of Cooper's Hawks. Based on studies of other accipiters, we also expected juvenile mortality of Cooper's and Sharp-shinned hawks to be greater than that of adults.

## METHODS

*Study site.*—Our study site was centered in Vigo County in west-central Indiana and the adjacent counties in Indiana and eastern Illinois. The site included both urban and rural areas. Our urban area was centered at Terre Haute, Indiana (pop. 60,000; 39° 27.1' N, 87° 18.5' W) and covered approximately 40 km<sup>2</sup>. There, we focused on Cooper's Hawks, mainly during the winter seasons of 1999–2001 (see also Roth and Lima 2003); one Cooper's Hawk was also tracked into the urban site during the winter of 2003–2004. Approximately 30% of this area consisted of high-density residential and commercial properties (>14 buildings/block), whereas the remaining 70% encompassed lower-density residential areas (<14 buildings/block; Topologically Integrated Geographic Encoding and Referencing [TIGER] data, U.S. Census Bureau, Geography Division 2000, <http://www.census.gov/geo/www/tiger/>). Although we attempted to study Sharp-shinned Hawks in this urban setting, none could be trapped and few were observed.

Our rural area included all areas adjacent to, and mainly west of, the Wabash River, which is to the immediate southwest of our urban area. Here, we focused mainly on Sharp-shinned Hawks during the winter seasons of 2000–2004, but also tracked several Cooper's Hawks. Northern Goshawks were not included in this study, as they are very rare in west-central Indiana; only one was observed during the 5-year study, and only one has been recorded during the 45 years of the local Christmas Bird Count (P. E. Scott pers.

comm.). The rural study area covered approximately 1,000 km<sup>2</sup> and included small clusters of houses, agricultural land, and fragmented forest. The landscape was composed of approximately 3.7% residential, 48% agricultural field (bare in winter), 17.9% grass/fallow field, 24.9% upland forest, 3.7% bottomland forest, 0.4% wetland, and 1.4% water (lakes, ponds, river).

**Capture and tracking.**—Using constantly monitored bal-chatri traps (Berger and Mueller 1959) and bow nets, we conducted trapping from late November through late January during each winter. Traps were baited with European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*). We positioned traps in open areas, along potential travel paths, and at potential roost locations used by accipiters. For example, in the city, we commonly trapped in parking lots, cemeteries, and recreational parks, and, in the rural area, we trapped in bare fields, along roadsides and power lines, and at a few long-established bird feeders. We recaptured only one individual during the study, whereupon we removed the transmitter and harness and examined the hawk for signs of transmitter-related stress. Once captured, our accipiters assiduously avoided traps on future encounters (TCR and SLL pers. obs.).

We used radio-telemetry to track hawks. Hawks were fitted with 2.4- to 11.0-g position-sensitive transmitters (models BD-2P, PD-2P, and RI-2CP; Holohil Systems, Carp, Ontario, Canada; Sharp-shinned Hawks: male, 2.4 g; female, 3.5–4.5 g; Cooper's Hawks: male, 4.2–5.8 g; female, 6.9–11.0 g) using the pelvic harness technique of Rappole and Tipton (1994; see also Roth and Lima 2003). In all cases, transmitter mass was <3% (mean = 2.09% ± 0.09 SE) of the hawk's total body mass. Transmitters had a life expectancy of approximately 3 months (2.4-g model) to over 6 months (11.0-g model). A position-sensitive switch on the transmitters provided information on hawk posture (horizontal or vertical) and was instrumental in determining mortality. A stationary signal indicating that the transmitter was horizontal—with no fluctuation—was usually a good indication of mortality, which prompted attempts to conduct visual verification.

Tracking was usually conducted from the

day of capture until the hawk was found dead or had abandoned the study site, or until the transmitter failed. All hawks were tracked ≥2 hr (frequently up to 10 hr) daily from vehicles using yagi and whip antennae. In addition, activity was monitored at roosts 0.5 to 1 hr before sunrise and 0.5 to 1 hr after sunset. The primary purpose of this intensive tracking was to collect detailed behavioral data, such as diet, movement, and activity. Due to this intensive tracking, we are certain of the day during which a hawk died or left the study site. If a hawk's signal was lost, we verified its departure with systematic scanning of the entire study site for ≥7 days. We distinguished hawk departure from transmitter failure in two ways: (1) transmitters that were about to fail typically produced signature shifts in signal (C. J. Amlaner pers. comm.), and (2) transmitters lost due to harness failure were retrieved. The hawks did not demonstrate any evidence of disturbance by our presence in vehicles, so we assumed that our tracking did not provoke any movement from the site.

Sources of mortality were predation and accidents (collisions with windows and vehicles). Although we did not observe predation events, we used the condition of the kill to determine the probable cause of predator-induced mortality. Plucked remains in a neat pile suggested predation by an accipiter, most likely Cooper's Hawk (TCR and SLL pers. obs.), whereas remains that were mostly intact, but decapitated or cleanly cut in half (Houston et al. 1998, Mazur and James 2000) with large, triangular incisions, and/or those with crimped antenna, suggested owl predation. In most cases, we were able to recover the carcass within 12 hr of death (i.e., early the next morning when the hawk did not leave roost). We usually recovered the posterior portion of the carcass, as the transmitters were never removed from the body. All retrieved carcasses of hawks that had died during the night showed signs of predation; none had conical teeth marks or masticated bones. This is strong evidence that hawks were not scavenged by mammals during the night, but were killed on or near their roost by owls.

For deaths from collision, we used the location and condition of the carcass to identify the object with which the hawk collided. Remains found along a roadside with signs of

blunt trauma, but with no sign of predation, were considered vehicular-collision mortalities, whereas those found near a house and with no sign of predation, but with apparent trauma to the head, were considered window-collision mortalities. Although we observed some hawks collide with windows, none of the observed cases resulted in mortality. If we could not recover the remains within 1 day, we used the location of the kill to determine the probable cause of mortality (predation versus collision near house). If the location provided no clear indication of the cause of mortality, the cause was considered unknown.

*Survivorship analysis.*—We estimated survivorship using the Kaplan-Meier procedure (Kaplan and Meier 1958) with a Cox proportional hazard regression model (Cox 1972) to determine the effects of sex, age, and species on survival using Systat (SPSS, Inc. 1998). The Cox model produces a standard survivor function and permits the analysis of covariates with proportional shifts of the hazard function. We used sex and species as covariates of survival and stratified by age to distinguish differences between juveniles (hawks in their first year) and adults (hawks after their first year). A log-rank Mantel test was used to reveal differences between the age strata (SPSS, Inc. 1998). All data points were right censored when hawks left the study site as itinerants (birds lacking stable home ranges and possibly still migrating) or migrants (birds that moved north in March or April), or were lost for other reasons (e.g., transmitter failure). We do not include hawks depredated within 7 days of transmitter attachment (four cases), as these deaths were possibly related to capture, the transmitter, or the transmitter attachment and are possibly the result of preoccupation with the transmitter and the resulting lack of vigilance. In all hawks, transmitter “grooming” was minimal by the 2nd or 3rd full day of transmitter attachment; thus, the 7-day period was thought to be long enough to remove the effects of newly attached transmitters from the analysis.

## RESULTS

We captured and tracked 40 Sharp-shinned Hawks (40 rural, 0 urban) and 27 Cooper's Hawks (14 rural, 13 urban) during the 5-winter study. The sex ratio of captured hawks was

not significantly different from 1:1 for either species (Sharp-shinned Hawks: males = 18, females = 22,  $\chi^2 = 0.40$ ,  $df = 1$ ,  $P = 0.53$ ; Cooper's Hawks: males = 13, females = 14,  $\chi^2 = 0.04$ ,  $df = 1$ ,  $P = 0.85$ ), although the sex ratio of Cooper's Hawks differed between urban and rural habitats (urban: males = 2, females = 11; rural: males = 11, females = 3; Fisher exact test,  $P = 0.001$ ). The age ratio was biased toward immatures in both species and was not significantly different between species (Sharp-shinned Hawks: adult = 14, immature = 26; Cooper's Hawks: adult = 11, immature = 16;  $\chi^2 = 0.23$ ,  $df = 1$ ,  $P = 0.63$ ; Table 1).

Neither species nor sex were significant covariates of survivorship (log-likelihood  $\chi^2$  estimate = 1.98,  $df = 2$ ,  $P = 0.37$ ; sex:  $t < 0.001$ ,  $P > 0.99$ ; species:  $t = 1.36$ ,  $P = 0.17$ ). Adult survival was significantly higher than juvenile survival (Mantel method,  $\chi^2 = 4.42$ ,  $df = 1$ ,  $P = 0.036$ ). The probability of survival over the 110-day study period was 9.4% for juveniles and 75.4% for adults (Fig. 1). Mortality events occurred throughout the study up to 101 days after transmitter attachment; however, after the first 7 days, there was no evidence of increasing risk of mortality with time (Fig. 1). Although not significant, winter survival tended to be greater for Cooper's Hawks than for Sharp-shinned Hawks. Seven of 13 (53.8%) Cooper's Hawks with known fates survived the winter (i.e., itinerants and hawks with unknown fates removed from analysis), while only 8 of 23 (34.8%) Sharp-shinned Hawks survived (Table 1).

Many hawks appeared to be itinerant, as indicated by their lack of a stable home range (TCR and SLL unpubl. data) and eventual abandonment of the study site. Of the 27 Cooper's and 40 Sharp-shinned hawks captured, 5 (18.5%) and 11 (27.5%), respectively, left the study site (itinerants, Table 1). There was no significant effect of age on the tendency to be itinerant ( $\chi^2 = 0.39$ ,  $df = 1$ ,  $P = 0.53$ ); on the three occasions when itinerant hawks left as they were being tracked, all moved south of the study site at least 20–30 km before we lost their signal.

As we tracked hawks through the end of winter, we recorded the proportion of individuals (of those with functioning transmitters) that remained on the study site during the

TABLE 1. Fates of wintering Cooper's and Sharp-shinned hawks captured in west-central Indiana, 1999–2004.

	Cooper's Hawk			Sharp-shinned Hawk		
	Adult	Immature	Total	Adult	Immature	Total
Total no. of hawks captured	11	16	27	14	26	40
Fate determined (54% of captured hawks)						
Died						
Collision	0	3	3	1	2	3
Predation	0	3	3	3	9	12
Survived						
Migrated	1	1	2	4	4	8
Resident	2	3	5	—	—	—
Total determined fates	3	10	13	8	15	23
% mortality of hawks with determined fate	0.0	60.0	46.2	50.0	73.3	65.2
Fate undetermined (46% of captured hawks)						
Itinerant	4	1	5	3	8	11
Unknown	4	5	9	3	3	6
Total undetermined fates	8	6	14	6	11	17

breeding season (Table 1). Sharp-shinned Hawks do not routinely breed in western Indiana, and all surviving Sharp-shinned Hawks (8/8) migrated north in late March or early April. Approximately 70% (5/7) of Cooper's Hawks were residents, while the remaining birds (2/7) were migrants. Of the migrant Cooper's Hawks, one died after a collision with a window about 75 km north of the study site.

Predation was a major source of mortality. Of all hawks (excluding itinerants and hawks

with unknown fates), 23.1% (3/13) of Cooper's Hawks and 52.2% (12/23) of Sharp-shinned Hawks were killed by a predator (Table 1). Of all causes of mortality, predation accounted for 50% (3/6) among Cooper's Hawks (two by owl and one by an unknown predator) and 80% (12/15) among Sharp-shinned Hawks (six by owl, one by Cooper's Hawk, and five by unknown predators). This species-specific difference in predator-induced mortality was not significant (Fisher exact test,  $P = 0.29$ ). Additionally, four hawks (three Sharp-shinned, one Cooper's) were depredated within 7 days of transmitter attachment (as noted above, these individuals were not included in the survivorship analysis). All predation on Cooper's Hawks occurred in the rural site; only accidental death was observed in the urban site.

Collisions with windows and automobiles were the main sources of accidental mortality. In the urban area, we documented two fatal collisions, one each with a window and an automobile. We also observed several non-lethal collisions with windows. In two cases, it seemed that hawks were attempting to attack a competitor (their reflection) and, as a result, hit the window first with their talons. The impact of such collisions did not seem to cause problems for the hawks during the course of the study. An additional urban hawk flew into

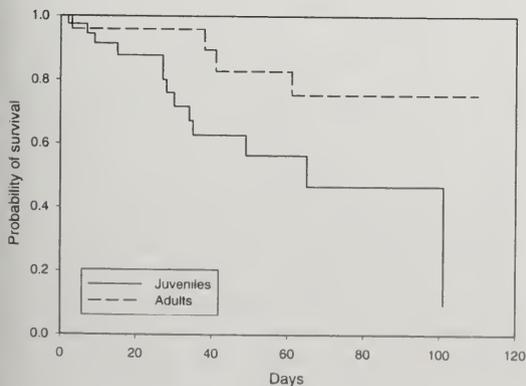


FIG. 1. Survivorship of wintering accipiters (Sharp-shinned and Cooper's hawks combined), by age class, in west-central Indiana, 1999–2004. Juvenile survival rate (solid line) is significantly lower than that for adults (dashed line;  $P = 0.036$ ) based on the Cox proportional hazard model. See text for details.

an open garage, apparently suffered head injuries, and died 1 day later. In the rural area, we recorded two fatal collisions with windows—one with an automobile and one with a boulder, possibly during an attack. The latter event may have been an indirect effect of the recently attached transmitter (collision occurred 3 days after attachment).

### DISCUSSION

The winter survivorship of Cooper's and Sharp-shinned hawks was approximately 9% for immatures and 75% for adults. Adult survival was significantly greater than that of immature hawks, but there was no significant effect of species or sex in the model. Mortality was caused predominantly by owl predation in the rural habitat and by accidents in the urban habitat.

The survival rates of adult Sharp-shinned and Cooper's hawks in our study fall within the range of those published elsewhere. Adult survivorship seems to be about 60–80% for most accipiters (Henny and Wight 1972, Boal 1997, Squires and Reynolds 1997, Tornberg and Colpaert 2001), and this is consistent with our results for the adults of both species. In addition, differences between juvenile and adult mortality have been observed in other accipiter populations such as Cooper's Hawks (Henny and Wight 1972, Boal 1997), Northern Goshawks (Kenward et al. 1999), and Sparrowhawks (Newton 1975; Newton et al. 1983, 1999). Although we also found age-related differences in accipiter mortality, juvenile survivorship (9.4%) in our study was lower than that typically reported for juvenile hawks elsewhere (20–50%; Henny and Wight 1972, Newton et al. 1983, Boal 1997, Kenward et al. 1999).

The high predation rates on juvenile hawks in our study might reflect a high site-specific abundance of owls, although we have no data on owl densities in our study area. Transmitter attachment also may have contributed to the low survival of juvenile hawks. We removed from our analyses four immature hawks that were depredated within the first 7 days of tracking, the period when we observed the greatest amount of excessive (>2 hr/day) transmitter grooming. Beyond this period, the survivorship functions of both adults and juveniles were generally linear. Given the po-

tential difficulties experienced by juveniles in hunting and avoiding predators, the added mass, handling, and possible distraction by the transmitter attachment may have negatively influenced juvenile hawks. We note, however, that adult survival was not unusually low and no mortality was observed due to starvation. In addition, Reynolds et al. (2004) found no effect of backpack transmitters on goshawks, supporting the notion that our transmitters did not have a detrimental effect on survival. Whereas we used a synsacral mount rather than a backpack, the effects on flight dynamics are likely similar. Although we cannot separate predation on food-stressed or weakened hawks from predation on healthy hawks, we noted no emaciated birds among our recoveries. Furthermore, close inspection of all recaptured (one) or recovered (eight) hawks revealed no apparent long-term influence of transmitters or harnesses on the health of hawks, with the exception of one ectoparasite infestation localized under the transmitter (this bird was killed in an accidental collision). Overall, we suspect that juvenile survivorship in our study site was genuinely quite low.

Nearly 25% of our captured hawks were apparently itinerant. These hawks failed to maintain stable home ranges and typically disappeared within 14 days of capture. On three occasions, we managed to track itinerant hawks as they moved southward, and typically lost their signals 20–30 km south of the study site. This suggests that itinerant hawks were still moving southward, even as late as January. Furthermore, the Wabash River runs north-south through the study site and migrating hawks use geographical features such as rivers during migration (Zalles and Bildstein 2000); therefore, the presence of the river may have contributed to the proportion of migrating itinerants in our study site.

Our results indicate interesting differences in survivorship and causes of mortality between urban and rural habitats, but the lack of Sharp-shinned Hawks in urban habitats and relatively small numbers of rural Cooper's Hawks limited our ability to draw firm conclusions. Predation was common in the rural area, but was not observed in the urban area, which was consistent with Boal's (1997) observations. In our study, the lack of predation in the urban area may have been due to a lack

of owls and the numerical dominance of the larger female Cooper's Hawks (but see Mannan et al. 2004). In the absence of owls, large female hawks do not face the same mortality risks as their rural counterparts. In fact, our urban Cooper's Hawks were much more likely to hunt roosting prey at night by using the illumination of urban lighting and the moon, than were rural hawks (TCR and SLL pers. obs.). Rural hawks, particularly Sharp-shinned Hawks, may have avoided hunting in dim light due to the increased risk of predation from owls. Furthermore, the incidence of deadly collisions with windows and cars (one each) is surprisingly low in the urban habitat, given the concentration of such hazards in urban areas. Overall, our urban area is probably not a sink habitat for wintering Cooper's Hawks; however, some urban studies have revealed extremely high rates of mortality among urban Cooper's Hawks (particularly nestlings) during the breeding season (Boal 1997, Boal and Mannan 1999), suggesting that urban areas may sometimes represent reproductive sinks.

One might expect Sharp-shinned Hawks to occur frequently in the city given the large potential prey base (i.e., House Sparrows; Roth and Lima 2003) and a probable owl-free environment (TCR and SLL pers. obs.). However, we observed very few urban Sharp-shinned Hawks. One possible explanation is that Sharp-shinned Hawks preferred the more dense vegetation typically found in our rural area. However, our rural Sharp-shinned Hawks frequently hunted in open areas such as near feeders and hedge rows where prey were abundant. Thus, we suggest that Sharp-shinned Hawks avoided the urban habitat for other reasons: predation and possibly competition. The abundance of large female Cooper's Hawks in our urban habitat made it dangerous for all 100- to 400-g birds (Roth and Lima 2003), including Sharp-shinned Hawks (we had one apparent case of a Cooper's Hawk depredating a Sharp-shinned Hawk in our rural study area). Thus, the smaller Sharp-shinned Hawk may have avoided the urban habitat due to a greater perceived risk of predation. In addition, urban Sharp-shinned Hawks may experience aggressive competition from Cooper's Hawks. Sharp-shinned Hawks frequently take larger prey, such as

starlings and Mourning Doves (*Zenaida macroura*; TCR and SLL unpubl. data), the main prey of urban Cooper's Hawks in our study area (Roth and Lima 2003).

Finally, our results suggest that future studies on the behavior of small wintering birds should consider the implications of intraguild predation in raptors. Owls are apparently a significant threat to rural hawks, especially Sharp-shinned Hawks, during the crepuscular periods. Thus, we would expect that rural hawks might reduce their activity during these periods unless food stressed. In fact, we observed a tendency for Sharp-shinned Hawks to leave roosts late (after sunrise) and return well before sunset (TCR and SLL unpubl. data; see also Sunde et al. 2003). Small birds may take advantage of periods when Sharp-shinned Hawks are not active by feeding early and late in the day, and feed less during the midday when both Sharp-shinned and Cooper's hawks are active. In addition, Cooper's Hawks are a potential threat to Sharp-shinned Hawks during most of the day. Sharp-shinned Hawks may reduce their activity in areas where Cooper's Hawks are abundant (e.g., urban habitat), thereby reducing the risk of predation experienced by smaller birds, such as sparrows (Roth and Lima 2003).

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## HABITAT USE BY RIPARIAN AND UPLAND BIRDS IN OLD-GROWTH COASTAL BRITISH COLUMBIA RAINFOREST

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**ABSTRACT.**—The value of riparian habitats to birds differs among ecosystems. I tested whether riparian habitat near large streams and rivers in the Pacific Northwest supported a higher abundance and diversity of birds than adjacent upland forest. From 1996 to 1998, I surveyed breeding birds at four 9-ha sites in coastal western hemlock forest on western Vancouver Island, British Columbia. Five species of forest generalists dominated both riparian and upland bird communities: Winter Wren (*Troglodytes troglodytes*), Chestnut-backed Chickadee (*Poecile rufescens*), American Robin (*Turdus migratorius*), Swainson's Thrush (*Catharus ustulatus*), and Pacific-slope Flycatcher (*Empidonax difficilis*). Species richness and total abundance were similar over the riparian-to-upland gradient, whereas abundances of riparian specialists and aerial foragers declined with distance from the river. To explore whether vegetation composition and structure explained bird distribution patterns, I sampled three locations along both riparian and upland transects at each site. Riparian areas had higher densities of deciduous trees; conifer and snag densities were higher in upland areas. Salmonberry (*Rubus spectabilis*) cover was marginally higher in riparian areas and blueberry (*Vaccinium* spp.) cover was higher in upland areas. There was little effect of distance from the river on most bird species, but there were stronger associations of birds with specific vegetation attributes. Tree and snag densities explained the most variation in abundance of aerial foragers, and eight of nine individual species, whereas distance from the river and shrub cover were important predictors of Hammond's Flycatcher (*Empidonax hammondi*) abundance. Apart from riparian specialists and a few species with strong vegetation associations, bird assemblages in riparian and upland habitats of this moist forest type were dominated by similar sets of generalist species. Received 1 December 2003, accepted 26 April 2005.

Riparian habitats are influenced by both stream channel processes and the adjacent upland vegetation (Brinson et al. 1981, Naiman et al. 1993). Topography, plant communities, hydrologic regimes, and soil type typically distinguish riparian areas from upland areas. Riparian habitats are heavily influenced by seasonal changes in water flow, and alluvial soils in riparian habitats tend to be wetter than soils in uplands. Riparian plant communities have diverse vegetation structures, high edge:area ratios, and are dominated by woody vegetation. These features are common to all riparian habitats, but vary greatly depending on geographical location. Riparian ecosystems often support high bird diversity and abundance (Thomas et al. 1979, Knopf et al. 1988, Anthony et al. 1996) because of their complex vegetation structure (LaRue et al. 1995, Wiebe and Martin 1998), high plant diversity (Bull 1978, Raedeke 1988), and proximity to water.

There is a strong bird diversity gradient from riparian to upland habitats in southwestern and agricultural regions of the U.S. (e.g., Stauffer and Best 1980, Szaro 1980, Knopf

1985, reviewed in Knopf and Samson 1994), where bird diversity is higher in riparian and lower in upland areas. In contrast, studies of mature, undisturbed stands in forests with greater annual precipitation (McGarigal and McComb 1992, Murray and Stauffer 1995, Wiebe and Martin 1998) have shown equal or lower diversity in riparian habitats compared with upslope habitats; these studies (McGarigal and McComb 1992, Murray and Stauffer 1995, Wiebe and Martin 1998), however, focused on riparian areas associated with small (<5 m wide) mountain streams. Some riparian areas show greater diversity near larger streams and rivers (Knopf and Samson 1994, Lock and Naiman 1998), and the avian use of riparian habitat relative to upland habitat along larger streams and rivers in the Pacific Northwest has not been well examined. I studied avian habitat use along larger streams and rivers within continuous undisturbed forest of the Pacific Northwest.

My first objective was to test the hypothesis that bird species diversity and abundance is higher in old-growth riparian habitat associated with large streams and rivers than in adjacent old-growth upland habitat. In the Pacific Northwest, riparian zones tend to be

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dominated by deciduous trees, whereas uplands are dominated by conifers (McGarigal and McComb 1992, Pearson and Manuwal 2001). Disproportionate use of riparian habitats by birds should be reflected in a decline in species richness and abundance with increasing distance from the river, but association with riparian habitat may vary among species and guilds. Riparian specialists that rely on the stream or river as a food source and nest near streams should decline in abundance with increasing distance from the river. Riparian forest edges along streams support a higher invertebrate biomass (Murakami and Nakano 2002), due to higher densities of aquatic insects (Murakami and Nakano 2002), and possibly greater primary productivity (Ranney et al. 1981). Aerial foragers such as flycatchers may respond to emergent aquatic insects near streams and rivers (Gray 1993) and should occur at highest densities near the water's edge. Conversely, conifer specialists may increase with distance from the river due to increasing conifer densities (McGarigal and McComb 1992, Pearson and Manuwal 2001).

Second, I explored how variation in vegetation composition and structure from riparian to upland habitat explains distribution patterns of several species. Studies conducted in other temperate coniferous forests have revealed differences in vegetation structure and composition between riparian and upland (McGarigal and McComb 1992, Pearson and Manuwal 2001). If the structural and species attributes of riparian vegetation communities are the primary predictors of bird diversity and abundance, then use of riparian habitats should be related to the prevalence of these structures relative to upland areas. Alternatively, bird diversity and abundance should not differ between riparian and upland habitats that are similar in vegetation structure and composition.

#### METHODS

*Study area.*—The study was conducted in three valleys on the west coast of Vancouver Island, British Columbia, between Ucluelet in the north and Bamfield in the south (48° 5' N, 125° 5' W). Four sites of continuous old-growth forest were selected along the Nahmint ( $n = 2$ ; 2 km apart), Taylor ( $n = 1$ ), and Klanawa rivers ( $n = 1$ ). The sites were em-

bedded within a mosaic of forest patches of different ages across a landscape in which the amount of primary forest varied from 50 to 70%. I classified rivers to stream order at a 1:50,000-map scale based on branching following Kuehne (1962). The Nahmint and Taylor rivers (fourth order) and the Klanawa River (fifth order) ranged in width from 15 to 57 m. Study sites were located in the Western Vancouver Island ecoregion, within the moist-to-very-wet maritime biogeoclimatic subzones of coastal western hemlock (Klinka et al. 1991, Nuszdorfer and Boettger 1994). The forest is dominated by amabilis fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) occur at their greatest densities adjacent to the rivers, but were also scattered throughout the forest in moister areas. The understory is dense, highly stratified, and contains shrubs such as salmonberry (*Rubus spectabilis*), red huckleberry (*Vaccinium parvifolium*), salal (*Gaultheria shallon*), and devil's club (*Oplopanax horridus*), with Alaskan (*Vaccinium alaskense*) and oval-leaf blueberry (*V. ovalifolium*) predominating in the upland areas. The climate is cool and wet in winter and warm and dry in late summer (July–September). Annual precipitation in the area averages 3,100 mm, and daily temperatures average 3.2° C in January and 15.6° C in July (Environment Canada Climate Data Services).

*Vegetation sampling.*—I sampled vegetation during 1995 within 20-m-radius circular plots (0.13 ha) using a procedure modified from James and Shugart (1970). I accounted for the large size of trees locally by increasing the plot radius (Mueller-Dombois and Ellenberg 1974, Bryant et al. 1993). To improve the accuracy of visual estimation over a large area, each plot was divided into four quadrats. I sampled vegetation in each of the four quadrats and then calculated means of the four quadrats for each variable. Plots were placed at three stations 150 m apart along two 500-m transects: one in riparian and one in upland habitat. Transects were oriented parallel to the river, 20 m (riparian) and 160 m (upland) from the river, for a total of six plots per site. Because previous studies indicate that both floristics and structural attributes play roles in avian habitat selection (MacArthur and Mac-

Arthur 1961, Holmes and Robinson 1981, Robinson and Holmes 1984), I focused on 10 variables representing broad measures of vegetation characteristics: density of deciduous and coniferous trees, snag density, volume of coarse woody debris (CWD), species richness, total percent cover of all shrubs and forbs, and percent cover of the two dominant shrubs (salmonberry and blueberry). Density (number/ha) was recorded for coniferous trees, deciduous trees, and snags within the entire 20-m-radius plot. Trees <3 m in height and ferns were treated as shrubs. Richness and percent cover of shrubs was sampled in a 10-m-radius subplot nested within 20-m circular plots. Richness and percent cover of forbs was sampled using four 1-m<sup>2</sup> quadrats placed at the center of shrub plots. CWD, defined as fallen logs >10 cm in diameter, was sampled at the point of intersection along the circumference of 20-m plots; I recorded diameter and length to calculate volume (m<sup>3</sup>/ha) of CWD (Van Wagner 1968, Thomas et al. 1979).

*Bird sampling.*—Details of bird sampling can be found in Shirley (2002). Briefly, birds were censused using a full-plot, area-search method (Slater 1994). A 9-ha grid was established at each site by running a 450-m line parallel and adjacent to the river's edge and nine perpendicular lines extending 200 m from the river. Grid lines were set 50 m apart and flagged at 25-m intervals. Censusing was conducted at each site by at least two observers who walked the grid lines from 05:00 to 10:00 (PST) on days without rain or high winds. We censused birds at each site four times each breeding season from 1 May to 15 July so that each site was censused once approximately every 2 weeks. Birds of prey and flyovers were not included in the censuses. I varied the order in which sites were sampled, and three to four observers rotated among sites and grid lines. To avoid double-counting, vocal and visual observations were recorded on site maps that were later evaluated to calculate number and relative abundance of bird species with respect to distance from the river. The numbers of observations over the four censuses in each year were averaged to provide a mean number of species and individuals per species for each site. I categorized observations into four distance categories from the river's edge (0–50, 51–100, 101–150, and

151–200 m) and calculated relative abundance for each distance category as the abundance averaged over 3 years and four sites.

I analyzed bird abundances by selected guilds and by individual species. I focused the guild analysis on two guilds that I predicted would show a gradient in abundance from riparian to upland: riparian specialists and aerial foragers. I assigned species to guilds after Hatler et al. (1978), Ehrlich et al. (1988), and Campbell et al. (1990, 1997) (Appendix). For individual species, I restricted my analysis to those with >5 observations in each year (nine species). When estimating species richness by site, I minimized the impacts of transient species by excluding species that were likely migrants and species observed in only one census session during each year (Willson and Comet 1996).

*Habitat associations.*—I used Akaike's Information Criterion corrected for small samples (AIC<sub>c</sub>) to select suitable models of association between vegetation variables and avian abundance (Burnham and Anderson 2002). I used multiple regression and estimated the residuals to model species richness and abundance of avian guilds and individual species as a function of vegetation variables. Models were based on *a priori* hypotheses of those vegetation variables that may be associated with a guild's or species' abundance. For each model, I computed AIC<sub>c</sub> and  $\Delta$ AIC<sub>c</sub>. Model likelihoods were standardized to sum to 1 and expressed as Akaike weights ( $\omega$ ). The Akaike weight can be considered as the weight of evidence supporting a given model as the best model; the higher the Akaike weight, the stronger the model. To identify plausible models for each species or guild, I ranked the Akaike weights of models in a given set to produce evidence ratios (i.e., the weight of the best model divided by that of a given model; Burnham and Anderson 2002). Evidence ratios express the likelihood of the selected model relative to other models.

*Data analysis.*—Vegetation attribute and avian abundance data were tested for normality using the Shapiro-Wilks statistic (Shapiro and Wilk 1965) before conducting paired *t*-tests and ANOVAs. Homogeneity of variances for one-way ANOVA and repeated-measures ANOVA were tested using the Levene and Bartlett-Box *F* tests, respectively (Norusis

1994). Species abundance data that violated these assumptions were either  $\log(y + 1)$  or rank transformed (Conover and Iman 1982). The  $\alpha$  level of significance was set at 0.10 to minimize the high biodiversity cost of making a type II error in resource management decisions (Toft and Shea 1983, Dayton 1998). I also define a level of "marginal significance" as  $0.15 > P > 0.10$ . All data were analyzed using SPSS for Windows 6.1.4 (Norusis 1994).

To compare riparian and upland means for each of the 10 vegetation variables, I used paired  $t$ -tests because riparian and upland habitats were paired by site for each of the four sites. Rather than correcting for multiple tests using the standard Bonferroni method, which has several disadvantages when gauging the effects of variables in ecological research (Nakagawa 2004), I present effect sizes as recommended by Hurlbert (1994). I evaluated the biological significance of the results using established criteria (Cohen 1988) where a small effect size = 0.2, medium = 0.5, and large = 0.8.

To compare abundances (all species combined, two guilds, and nine individual species) by distance category from the river and among years, I used a two-way, repeated-measures ANOVA, with year and distance from river's edge as fixed effects. Because the same sites were censused over 3 years, I treated year as a repeated variable in a model that specified polynomial contrasts to detect linear or quadratic trends over time (Gurevitch and Chester 1986, von Ende 1993). Because there were no significant year effects, data were pooled across years for all comparisons except for American Robin (*Turdus migratorius*), which showed a significant distance-by-year interaction. I then tested for differences in pooled abundance (one-way ANOVA; all species combined, two guilds, and eight species) across four 50-m intervals from the river's edge—with distance from edge as a fixed factor ( $n = 48$ ). For American Robin, I performed the above analysis for each year separately; however, results are presented for all years together (Fig 1). Effect sizes for the one-way ANOVAs were calculated using the Eta squared method (Levine and Hullett 2002).

Because there was a significant year effect for species richness, I did not pool data across

years. I compared species richness across the four 50-m intervals from the river's edge and over time using two-way, repeated-measures ANOVA with year and distance from edge as fixed factors ( $n = 16$ ).

## RESULTS

*Vegetation.*—Four of 10 measures of vegetation structure and composition—density of coniferous and deciduous trees, shrub-species richness, and blueberry cover—differed between riparian and upland habitats (Table 1). Effect sizes were medium for coniferous tree density and large for deciduous tree density, reflecting substantial biological differences. Riparian habitats had nearly five times the density of deciduous trees compared with upland areas, while upland areas had greater conifer density and percent blueberry cover. Snag density and salmonberry cover were greater in upland and riparian areas, respectively; effect sizes were large, but these differences were only marginally significant due to a small sample size. CWD and forb cover were not statistically different between habitats, but effect sizes were medium and could indicate biological significance.

*Avian abundance and diversity.*—During 1996–1998, I recorded 645 observations of 36 species. For all sites combined, there were >20 observations for 9 species, accounting for 80% of all observations. The five most abundant species were Winter Wren (*Troglodytes troglodytes*), Chestnut-backed Chickadee (*Poecile rufescens*), American Robin, Swainson's Thrush (*Catharus ustulatus*), and Pacific-slope Flycatcher (*Empidonax difficilis*). For all years and in each distance interval, assemblages were dominated by these five species, which composed 53–58% of total observations—with only minor variations in their abundance rankings. Except for one forest interior species (Pacific-slope Flycatcher), these species are forest generalists. Winter Wren and Chestnut-backed Chickadee were the dominant species in upland sections and were replaced, in part, by American Robin and Swainson's Thrush near the river. Riparian specialists generally occurred close to the river and at low abundances, with the exception of Hammond's Flycatcher (*Empidonax hammondi*).

Because the dominant species were forest

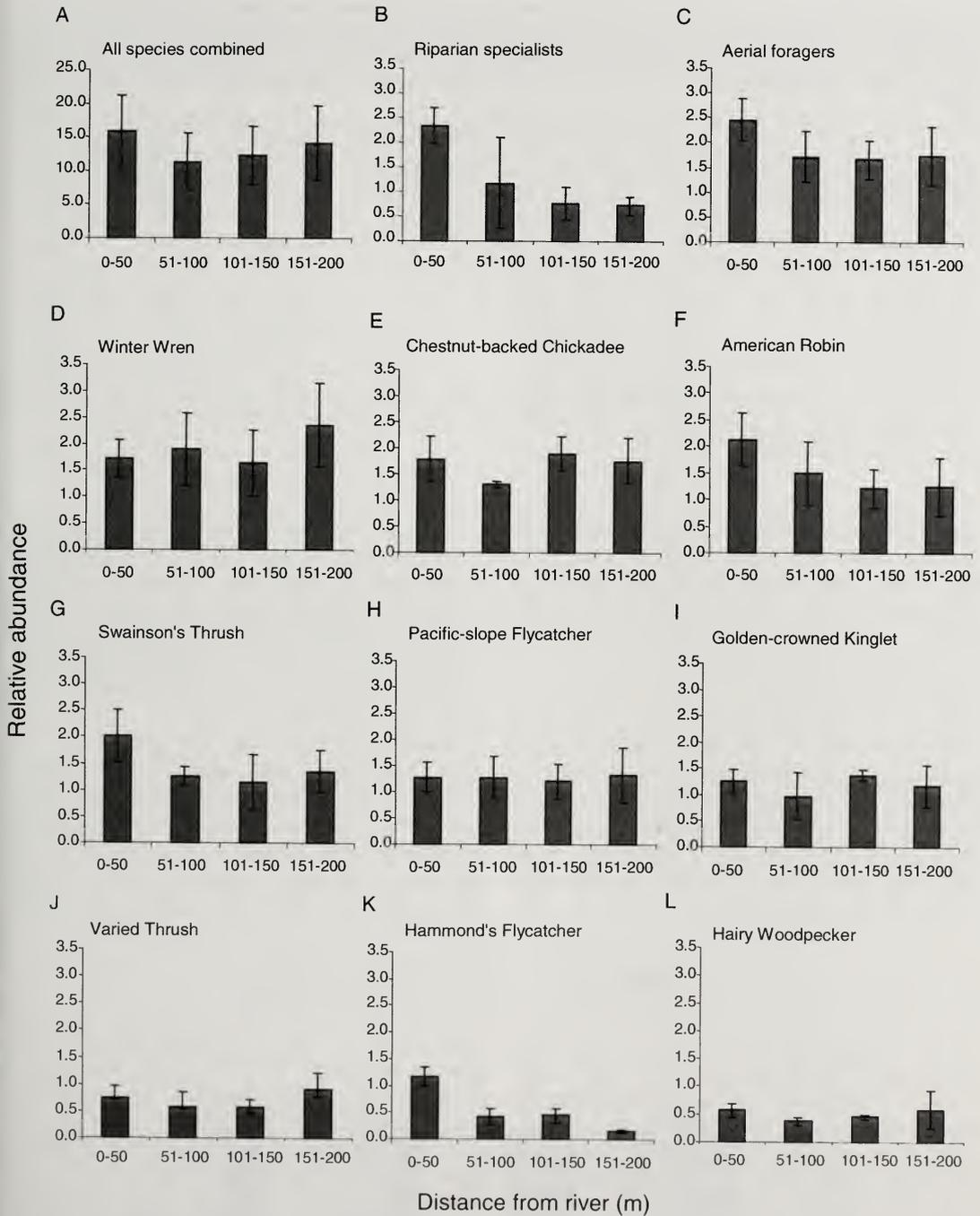


FIG. 1. Relative abundance (mean number of observations/site/year) and standard deviations (error bars) at 50-m intervals from the river's edge for (A) all species combined, (B) riparian specialists, (C) aerial foragers, (D) Winter Wren, (E) Chestnut-backed Chickadee, (F) American Robin, (G) Swainson's Thrush, (H) Pacific-slope Flycatcher, (I) Golden-crowned Kinglet, (J) Varied Thrush, (K) Hammond's Flycatcher, and (L) Hairy Woodpecker, 1996–1998, western Vancouver Island, British Columbia, Canada ( $n = 48$ ).

TABLE 1. Vegetation characteristics of riparian and upland habitats, western Vancouver Island, British Columbia, 1995. Of 10 variables, four (deciduous and coniferous tree densities, shrub species richness, and percent cover of blueberry species) differed ( $P < 0.10$ ) between riparian and upland habitats ( $n = 12$  for all tests).

Variable	Riparian mean (SD)	Upland mean (SD)	Paired <i>t</i> -test	<i>P</i>	Effect size <sup>a</sup>
Coniferous trees (no./ha)	247 (166)	356 (140)	-1.83	<b>0.095<sup>b</sup></b>	-0.45
Deciduous trees (no./ha)	288 (102)	59 (37)	4.06	<b>0.002<sup>b</sup></b>	0.79
Snags (no./ha)	72 (41)	134 (96)	-1.77	0.10 <sup>c</sup>	-0.88
Shrub cover (%)	27 (6)	25 (6)	0.80	0.44	0.06
Shrub richness (no. of species)	6 (2)	5 (2)	2.45	<b>0.092<sup>b</sup></b>	0.17
Salmonberry cover (%)	8 (7)	3 (3)	1.65	0.13 <sup>c</sup>	0.56
Blueberry cover (%)	2 (3)	5 (5)	-2.37	<b>0.098<sup>b</sup></b>	-1.53
Forb cover (%)	44 (24)	57 (17)	-0.80	0.48	-0.38
Forb richness (no. of species)	11 (3)	9 (4)	1.51	0.23	0.06
CWD (m <sup>3</sup> /ha)	2,512 (208)	3,549 (1,512)	-0.94	0.37	-0.41

<sup>a</sup> Effect size, measured as  $(m_1 - m_2)/m_1$ , where  $m_1$  = mean in riparian habitat and  $m_2$  = mean in upland habitat (after Hurlbert 1994).

<sup>b</sup> Bold-faced values denote significance at  $P < 0.10$ .

<sup>c</sup> Marginally significant ( $0.15 > P > 0.10$ ).

generalists, total abundance did not differ with distance from the river ( $F_{3,44} = 1.26$ ,  $P = 0.30$ ; Fig. 1A). As expected, abundances of riparian specialists and aerial foragers declined with distance from the river (Fig. 1B, C; riparian specialists:  $F_{3,44} = 7.98$ ,  $P < 0.001$ ; aerial foragers:  $F_{3,44} = 5.23$ ,  $P = 0.027$ ). Of the nine species for which I had sufficient data for analysis, only two varied significantly in abundance across the distance intervals: Swainson's Thrush ( $F_{3,44} = 2.85$ ,  $P = 0.10$ ; Fig. 1G) and Hammond's Flycatcher ( $F_{3,44} = 11.74$ ,  $P = 0.001$ ; Fig. 1K) were more common near rivers (all other species:  $P \geq 0.31$ , effect sizes  $< 0.07$ ).

Species richness did not differ with distance from the river ( $F_{3,12} = 0.15$ ,  $P = 0.93$ ) and there was no significant interaction between distance and year ( $F_{6,24} = 0.61$ ,  $P = 0.62$ ). Species richness, however, differed among years ( $F_{2,24} = 6.28$ ,  $P = 0.028$ ); 14% more species were detected in 1997 than in 1996 and 1998 (Fig. 2).

*Habitat associations.*—For most bird species, associations with specific vegetation attributes were stronger than with distance from the river. The best model for aerial forager abundance was one showing a negative relationship with conifer density (Table 2). This model was strongly supported ( $\omega_i = 0.850$ ),

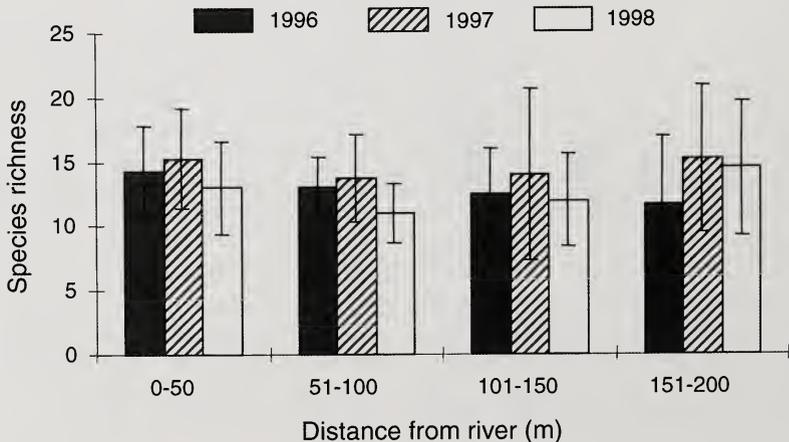


FIG. 2. Means and standard deviations (error bars) of avian species richness at 50-m intervals from the river's edge, 1996–1998, western Vancouver Island, British Columbia, Canada.

TABLE 2. Habitat model selection using Akaike's Information Criterion for abundance of avian guilds and species in undisturbed forest sites, western Vancouver Island, British Columbia, 1996–1998. Selected models with the highest likelihood are shown. Secondary models are included if they were nearly equal to the first model.

Guild or species	Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	ΔAIC <sub>c</sub> <sup>c</sup>	K <sup>d</sup>	ω <sub>i</sub> <sup>e</sup>
Aerial foragers	CT	-5.089	0.000	3	0.850
Riparian specialists	DI	27.940	0.000	3	0.244
	SA	28.221	0.281	3	0.212
	SH	28.444	0.504	3	0.190
	SR	28.911	0.971	3	0.150
American Robin	CT	27.795	0.000	3	0.405
Chestnut-backed Chickadee	CT	25.831	0.000	3	0.387
	SN	25.885	0.054	3	0.376
Golden-crowned Kinglet	CT	16.730	0.000	3	0.334
Hammond's Flycatcher	DI	20.110	0.000	3	0.396
	SH	20.165	0.554	3	0.385
	CT	6.963	0.000	3	0.533
Pacific-slope Flycatcher	CT	22.379	0.000	3	0.545
Swainson's Thrush	VA	21.764	0.000	3	0.266
	DT	21.932	0.168	3	0.244
	CT	22.065	0.301	3	0.229
	SN	9.212	0.000	3	0.457
Varied Thrush	SN	9.212	0.000	3	0.457
Winter Wren	CT	28.025	0.000	3	0.311

<sup>a</sup> CT = density of coniferous trees, DI = distance from river, DT = density of deciduous trees, SA = percent salmonberry cover, SH = percent shrub cover, SN = snag density, SR = shrub species richness, VA = percent blueberry spp. cover.

<sup>b</sup> Akaike's Information Criterion corrected for small sample sizes.

<sup>c</sup> ΔAIC<sub>c</sub> = difference between best model and model with minimum AIC<sub>c</sub>.

<sup>d</sup> Number of parameters.

<sup>e</sup> ω<sub>i</sub> = Akaike weight.

being 14 times more likely than the second-best model in the set. Abundance of riparian specialists was predicted equally by four single-variable models showing positive relationships with salmonberry, percent shrub cover, and shrub species richness, as well as a negative relationship with distance from the river. Support for all four models, however, was weak (all four ω<sub>i</sub> < 0.250) and the best model was only 2.5 times more likely than the next-best model in the set.

The abundances of four species (American Robin, Hairy Woodpecker [*Picoides villosus*], Pacific-slope Flycatcher, and Winter Wren) were best predicted by single-variable models showing negative relationships with conifer density (Table 2). Models for Hairy Woodpecker and Pacific-slope Flycatcher had moderate support (ω<sub>i</sub> = 0.533 and ω<sub>i</sub> = 0.545), being 3–4 times more likely than the second-best models in the sets. The models for American Robin and Winter Wren had weaker support (ω<sub>i</sub> = 0.405 and ω<sub>i</sub> = 0.311) and were only twice as likely as the second model in the set. Chestnut-backed Chickadee abun-

dance was best predicted by two single-variable models showing negative relationships with conifer (ω<sub>i</sub> = 0.387) and snag densities (ω<sub>i</sub> = 0.376); both models had almost equal support and were 3 times more likely than the third model in the set. Golden-crowned Kinglet (*Regulus satrapa*) abundance was best predicted by a model showing a positive relationship with conifer density; however, this model was relatively weak (ω<sub>i</sub> = 0.334) and only 1.3 times more likely than the second model in the set. Hammond's Flycatcher abundance was best predicted by two single-variable models representing a negative relationship with distance from the river (ω<sub>i</sub> = 0.396) and a positive relationship with percent shrub cover (ω<sub>i</sub> = 0.385). Both models had almost equal support and were 5 times as likely as the third model in the set. Swainson's Thrush abundance was best predicted by three single-variable models showing negative relationships with percent blueberry cover (ω<sub>i</sub> = 0.266) and density of coniferous trees (ω<sub>i</sub> = 0.244) and a positive relationship with density of deciduous trees (ω<sub>i</sub> = 0.229). The models

had almost equal support, although support for any one was quite weak. The best model for Varied Thrush (*Ixoreus naevius*) abundance showed a positive relationship with snag density ( $\omega_i = 0.457$ ). This model had moderate support, being 4 times as likely as the second model in the set.

#### DISCUSSION

*Species diversity and abundance along the riparian gradient.*—Contrary to my original predictions, species abundance and diversity of birds were similar along a distance gradient away from the river. Although species richness varied among years, total abundance remained similar during the study. Other studies in coniferous forests of the Pacific Northwest have also found that riparian areas do not support higher numbers of bird species or individuals (McGarigal and McComb 1992, Murray and Stauffer 1995, Pearson and Manuwal 2001). In contrast, studies in more arid or agricultural environments (Carothers et al. 1974, Stevens et al. 1977, Wauer 1977, Stauffer and Best 1980) found large differences in diversity and abundance between riparian and upland habitats. McGarigal and McComb (1992) proposed three hypotheses to account for the regional difference in these patterns: (1) high stream density and availability of water in upland areas in the Pacific Northwest, (2) a less pronounced microclimatic gradient (moderated by maritime influences) in northwestern forests, and (3) a more subtle transriparian gradient in vegetation structure. Higher rainfall and less variation in annual temperatures on western Vancouver Island compared with Washington and Oregon may produce an even less pronounced transriparian gradient.

In this study, riparian habitats had greater densities of deciduous trees, and the understory was dominated by salmonberry. In contrast, upland areas had higher densities of coniferous trees, and blueberry species dominated the shrub understory; uplands also tended to have greater snag densities. While low statistical power may have limited my ability to detect statistically significant differences in some attributes, my results are consistent with those of other studies that evaluated vegetation structure across the transriparian gradient of forests in the Pacific Northwest (McGarigal and McComb 1992, Pearson and Manuwal

2001). McGarigal and McComb (1992) attributed lower bird species richness in riparian as opposed to upland areas to the scarcity of conifers found along streams; however, in my study, conifers were not as scarce along riparian areas, perhaps accounting for the similarity in species richness between the two habitats. The lack of a strong gradient in vegetation structure from riparian to upland is also reflected in the distribution of the most common bird species. Abundances of eight of the most common bird species, as well as abundance of the aerial foraging guild, were associated most closely with densities of certain canopy and understory species rather than distance from the river. Complex topography, combined with consistently moist conditions, provides suitable habitat for most species across the riparian-upland gradient that I studied, and it probably accounts for the lack of strong riparian effects at the community level.

The large fourth- or fifth-order streams and rivers in my study area contrast with the smaller, second-order streams that were the focus of some previous studies in northern forests (McGarigal and McComb 1992, Wiebe and Martin 1998). In those studies, riparian forests supported equal or fewer species and individuals compared with surrounding uplands (McGarigal and McComb 1992, Wiebe and Martin 1998). Studies of larger-order streams, however, have indicated that they support denser, more complex riparian vegetation communities and greater avian density, species richness, and abundance (Knopf 1985, Lock and Naiman 1998). Lock and Naiman (1998) found greater species richness and abundance along larger rivers where the riparian habitat contained a higher ratio of deciduous to coniferous vegetation; in my study, however, avian species richness and abundance were similar across the riparian to upland gradient, even along larger streams. Most species used both riparian and upland habitats, whereas only a few species specialized in either habitat. In northwestern forests, these specialists represented a small fraction of the overall community.

*Habitat selection.*—Of the 36 species recorded, five occurred only near the river. Four of these riparian specialists—Common Merganser (*Mergus merganser*), American Dipper (*Cinclus mexicanus*), Belted Kingfisher (*Cer-*

*yle alcyon*), and Spotted Sandpiper (*Actitis macularius*)—depend on stream invertebrates and/or fish as food resources and they nest in adjacent riparian vegetation or riverbanks (Enns et al. 1993, Campbell et al. 1997). The remaining species, Willow Flycatcher (*Empidonax traillii*), rarely occurs in mature forest except in riparian areas. In the coastal western hemlock zone, Willow Flycatchers more commonly occur in marshes and early successional clearcuts (5–10 years of age) associated with young red alder and willow trees (Enns et al. 1993, Campbell et al. 1997).

Five species occurred only at single sites in upland sections of forest: Fox Sparrow (*Passerella iliaca*), Hutton's Vireo (*Vireo huttoni*), Olive-sided Flycatcher (*Contopus cooperi*), Spotted Towhee (*Pipilo maculatus*), and Yellow Warbler (*Dendroica petechia*). All of these species are rare in mature forests and may select large patches of open, deciduous vegetation in forest interiors.

As predicted, I found that aerial foragers declined in abundance with increasing distance from the river. Aerial foragers include Hammond's Flycatcher, a species that occupies a wide variety of habitats (Willson and Comet 1996). Throughout much of the Pacific Northwest, the species is an upslope specialist that is associated strongly with conifers at sites characterized by relatively open canopies (Sakai and Noon 1991, McGarigal and McComb 1992); however, farther north in Alaska it favors deciduous stands (Willson and Comet 1996), and in the forests of Vancouver Island (Waterhouse and Harestad 1999, Shirley 2002) and southeastern British Columbia (Kinley and Newhouse 1997), this species is largely restricted to mixed riparian forests that include large deciduous trees and conifers. Whereas Hammond's Flycatcher may use riparian habitat, it is sympatric with the Pacific-slope Flycatcher in old-growth forest (Campbell et al. 1997) and its distribution may reflect some habitat partitioning between the two species. In southern Colorado, where Hammond's and Cordilleran (*Empidonax occidentalis*) flycatchers co-occur, Hammond's Flycatcher densities were approximately one-half those of the Cordilleran Flycatcher (Beaver and Baldwin 1975). In these areas of overlap, Hammond's Flycatcher inhabited aspen habitat, while the Cordilleran Flycatcher used

aspen-conifer habitat. Behavioral observations by Sakai and Noon (1991) suggested that some competition likely occurs between the Hammond's and Pacific-slope flycatchers, but it does not result in competitive exclusion of one species by the other. Pacific-slope Flycatcher abundance differed little along the gradient of distance away from the river, a reflection of its association with large conifer trees in both riparian and upland habitats. Interestingly, studies farther south in the Pacific Northwest (McGarigal and McComb 1992, Pearson and Manuwal 2001) reported that Pacific-slope Flycatchers are associated with riparian habitats, whereas Hammond Flycatchers are associated with upland habitats. The reason for this difference is unclear, but may relate to differences in species composition and size distribution of trees in the two forest habitats. For example, in the previous studies, large-diameter conifers required by Hammond's Flycatchers (Sakai and Noon 1991), such as Douglas-fir (*Pseudotsuga menziesii*), occur in greater numbers in upland forests.

Several of the dominant species in my study, including Chestnut-backed Chickadee and Golden-crowned Kinglet, showed associations with conifer or snag density. An exception was the Swainson's Thrush, which, although a forest generalist, was more abundant in riparian habitat. This species is widespread on the west coast (Campbell et al. 1997) and often forages in salmonberry and devil's club in riparian habitats. The positive association with deciduous trees suggests that these structures or some other closely associated vegetation may be an important influence on habitat selection for this species. Furthermore, virtually all Swainson's Thrush nests encountered incidentally during surveys ( $n = 8$ ) were found in salmonberry (SMS pers. obs.), suggesting a strong association with this shrub for nesting habitat and/or food.

*Management implications.*—Patterns of avian diversity and abundance in riparian communities often have been explained by dramatic gradients in microclimate and vegetation structure or composition (Carothers et al. 1974, Stevens et al. 1977, Dickson 1978, Szaro 1980). Where these gradients are subtle, as in forests of the Pacific Northwest, the patterns disappear (Wiebe and Martin 1998, Pearson and Manuwal 2001) or they may re-

verse—upland areas supporting greater diversity and abundance than riparian areas (McGarigal and McComb 1992). Northwest forests generally lack a strong microclimatic gradient from riparian to upland (Brososke et al. 1997), and ephemeral streams or ponds occur in virtually every upland area. These factors create a fine-scale habitat mosaic in which patches dominated by conifers are interspersed with deciduous trees and shrubs that provide habitat for species more typical of deciduous-tree-dominated riparian areas.

Recent discussions of land management practices to preserve native biodiversity of forest species include using a landscape-level approach that protects both riparian and upland habitats to ensure connectivity across the landscape (McGarigal and McComb 1992, Wiebe and Martin 1998). Maintaining connectivity may prevent isolation of remnant forest patches (Fahrig and Merriam 1985, Saunders and de Rebeira 1991, Gonzalez 2000); however, the lack of upland specialists in my study argues against placing too much emphasis on upland areas *per se*. Unmanaged riparian areas not only provide habitat for those few species that associate with specific features at the river's edge, they also contain habitat elements such as large conifers and snags important to many common forest species.

My study was limited in several ways that should be considered in the development of land use plans. First, although the contrast between riparian and upland habitats is known to be subtle in the moist forests of the Pacific Northwest (McGarigal and McComb 1992, Pearson and Manuwal 2001), differences in structure and composition of vegetation in my study may have been obscured by the small sample size and resulting lack of statistical power. Statistically, several of the vegetation characteristics that I measured were marginally or non-significant, but their medium to large effect sizes indicate possible biological significance. Second, comparisons in this study were limited to measures of avian abundance. Future work should focus on measures of relative fitness or productivity in the two habitats. Third, my study was conducted during the breeding season; work is also needed to assess avian distributions during other seasons, as the relative value of riparian and upland habitats may differ between periods of

migration and other seasons (Harris 1984, Wiebe and Martin 1998). For example, riparian habitats may provide critical habitat for Neotropical migrants as they travel between their wintering and breeding grounds (Stevens et al. 1977, Finch 1991), and riparian habitat may be important for the survival and population stability of migratory species during the breeding season. The diversity and density of some migrants may be greater in riparian corridors because they are easy to follow and/or provide diverse foraging habitats (Wiens 1989, Wiebe and Martin 1998).

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APPENDIX. Guild classification of avian species  
(after Hatler et al. 1978; Ehrlich et al. 1988; Campbell  
et al. 1990, 1997).

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Guild/Species

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Aerial foragers

- Hammond's Flycatcher (*Empidonax hammondii*)
- Olive-sided Flycatcher (*Contopus cooperi*)
- Pacific-slope Flycatcher (*Empidonax difficilis*)
- Willow Flycatcher (*Empidonax traillii*)

Riparian specialists

- American Dipper (*Cinclus mexicanus*)
  - Belted Kingfisher (*Ceryle alcyon*)
  - Common Loon (*Gavia immer*)
  - Common Merganser (*Mergus merganser*)
  - Hammond's Flycatcher (*Empidonax hammondii*)
  - Spotted Sandpiper (*Actitis macularius*)
  - Warbling Vireo (*Vireo gilvus*)
  - Yellow Warbler (*Dendroica petechia*)
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## DENSITY AND DIVERSITY OF OVERWINTERING BIRDS IN MANAGED FIELD BORDERS IN MISSISSIPPI

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**ABSTRACT.**—Grassland bird populations are sharply declining in North America. Changes in agricultural practices during the past 50 years have been suggested as one of the major causes of this decline. Field-border conservation practices encouraged by the U.S. Department of Agriculture's National Conservation Buffer Initiative meet many of the needs of sustainable agriculture and offer excellent opportunities to enhance local grassland bird populations within intensive agricultural production systems. Despite the abundant information on avian use of, and reproductive success in, strip habitats during the breeding season, few studies have examined the potential value of field borders for wintering birds. We planted 89.0 km of field borders (6.1 m wide) along agricultural field edges on one-half of each of three row crop and forage production farms in northeastern Mississippi. We sampled bird communities along these field edges during February–March 2002 and 2003 using line-transect distance sampling and strip transects to estimate density and community structure, respectively. We used Program DISTANCE to estimate densities of Song (*Melospiza melodia*), Savannah (*Passerculus sandwichensis*), and other sparrows along bordered and non-bordered transects while controlling for adjacent plant community. Greater densities of several sparrow species were observed along most bordered transects. However, effects of field borders differed by species and adjacent plant community types. Diversity, species richness, and relative conservation value (a weighted index derived by multiplying species-specific abundances by their respective Partners in Flight conservation priority scores) were similar between bordered and non-bordered edges. Field borders are practical conservation tools that can be used to accrue multiple environmental benefits and enhance wintering farmland bird populations. Provision of wintering habitat at southern latitudes may influence population trajectories of short-distance migrants of regional conservation concern. Received 4 October 2004, accepted 13 June 2005.

Grassland birds are one of the most sharply declining groups of birds in North America (Knopf 1994, Herkert 1995, Peterjohn and Sauer 1999). Grassland birds experienced a 1.1% per year decline from 1966 to 2002 in the U.S. and a 2.3% per year decline in the southeastern (U.S. Fish and Wildlife Service Region 4) U.S. (Sauer et al. 2003). Many grassland species are now associated closely with agricultural production systems because most (>80%) of the native grasslands in North America have been converted to other uses (Samson and Knopf 1994, Noss et al. 1995, Hunter et al. 2001), principally agricultural production. Although agriculture facilitated range expansions for several grassland species through clearing of forested land (Askins 1999, Arcese et al. 2002), several correlative studies now suggest agricultural intensification as a leading cause of decline for most grassland birds (Vickery et al. 1999, Blackwell and Dolbeer 2001, Murphy 2003).

Numerous changes in production agriculture have occurred within the past 50 years, hastening the decline of grassland birds. Most notable has been the shift from diversified, small-scale farms to large-scale, highly specialized, chemical- and capital-intensive monoculture farming systems. This shift has resulted in the loss of field edge, fencerow, and other non-crop herbaceous communities (Rodenhouse et al. 1993, Warner 1994, Koford and Best 1996). Recent changes in Conservation Reserve Program (CRP) enrollment options (continuous sign-up) now permit partial field enrollments, thus encouraging conservation-oriented production practices (e.g., conservation buffers) without removing an entire field from production. Conservation buffer practices, available in several Farm Bill conservation programs, offer valuable opportunities to create habitat for grassland birds within intensively farmed landscapes. Grassed waterways, contour grass strips, filter strips, riparian buffers, crosswind trap strips, windbreaks, and shelterbelts are conservation buffer practices used to reduce soil erosion (Dillaha et al. 1989), diminish herbicide and nutrient runoff

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into wetlands (Daniels and Williams 1996, Webster and Shaw 1996), and provide wildlife habitat (Bryan and Best 1991, Puckett et al. 1995, Marcus et al. 2000).

Within intensively farmed landscapes, conservation buffers are increasingly the only available semi-permanent grasslands for nesting birds (Warner 1994, Koford and Best 1996). Field borders, defined as intentionally managed herbaceous plant communities along crop field edges to provide environmental and wildlife habitat benefits, are another type of conservation buffer practice. However, unlike conservation buffer practices specifically designed to filter sediments, field borders may be more broadly applied than simply along downslope edges of fields. Field borders may be established where other conservation buffer practices do not meet eligibility criteria, are not cost effective or practical, or are not desired by the producer.

Although herbaceous strip habitats may have limited value as nesting cover because reproductive success is low (Basore et al. 1986, Bryan and Best 1994, Camp and Best 1994), field borders may provide important wintering habitat for numerous short-distance migrants that winter in the southern U.S. Several studies have documented grassland bird use and reproductive success within other agricultural edge habitats (Best 1983, Johnson and Beck 1988, Best et al. 1990, Sparks et al. 1996); however, no studies have addressed explicitly the importance of field borders. Furthermore, most studies of grassland birds have been conducted during the breeding season (Rodenhouse et al. 1993, Herkert et al. 1996, Ryan et al. 1998, Peterjohn 2003). Only Marcus et al. (2000), in North Carolina, addressed the benefits of field borders to wintering birds. Ryan et al. (1998) noted the lack of data detailing winter bird use of CRP fields, and wintering habitat requirements and ecology of most grassland birds are poorly known (Vickery et al. 1999). Herkert et al. (1996) and Peterjohn (2003) contend that the paucity of information on wintering grassland birds limits our ability to develop effective conservation strategies for them.

Our objectives were to estimate the effects of field borders on grassland bird density and diversity during the winter in northeastern Mississippi. We also characterized avian com-

munity structure in bordered and non-bordered fields, relative to adjacent plant communities.

## METHODS

*Study area.*—Our study was conducted on three privately owned farms in Clay and Lowndes counties (88° 32' W, 33° 34' N), located within the Black Prairie physiographic region of northeastern Mississippi. All farms in the region have a history of agricultural use, most having actively produced crops for >50 years. Primary agricultural production included soybeans (*Glycine max*), corn (*Zea mays*), forage, and livestock. Most row-crop fields on all three study farms were tilled in late fall in preparation for spring planting. The farms were selected based on similarities in cropping practices, landscape composition (approximately 60–80% row crop), soil associations, and landowner cooperation.

Grasslands on each farm consisted predominantly of perennial, exotic, cool-season forage grasses (tall fescue, *Festuca arundinacea*) and warm-season exotics (Bermudagrass, *Cynodon dactylon*; and Bahia grass, *Paspalum notatum*; Smith 2004). Small remnant and reintroduced stands of native grasses (big bluestem, *Andropogon gerardii*; little bluestem, *Schizachyrium scoparium*; and broomsedge, *A. virginicus*) were scattered throughout each farm. Fencerows, drainage ditches, and contour filter strips were dominated by tall fescue and Johnson grass (*Sorghum halepense*). Periodically disturbed areas contained early seral-stage grasses and forbs (paspalum, *Paspalum* spp.; panicgrass, *Panicum* spp.; giant ragweed, *Ambrosia trifida*; annual marshelder/ sumpweed, *Iva annua*; Johnson grass; and goldenrod, *Solidago* spp.). Wooded areas were predominantly oak (*Quercus* spp.), green ash (*Fraxinus pennsylvanica*), maple (*Acer* spp.), hickory (*Carya* spp.), sugarberry (*Celtis laevigata*), and eastern redcedar (*Juniperus virginiana*; Smith 2004).

During early spring 2000, we established experimental field borders (6.1 m wide) along row-crop field margins (fencerows, drainage ditches, access roads, and contour filter strips) on one-half of each farm. Mean field size was 26.9 ha ( $n = 37$ , range = 2.9–146.9) and mean percentage of the field area given over to field borders was 6.0% (range = 0.5–15.3).

Overall, field borders (54.3 ha) composed 0.8–1.3% of the land area of bordered sections of each farm. In return, producers were paid an initial \$247.10/ha sign-up bonus with a \$123.55/ha/year rental rate for land dedicated to field borders. Producers were required not to mow, treat with herbicide, or disk field borders during the duration of the study. Initially, field borders were seeded with a Kobe lespedeza (*Lespedeza striata*) and partridge pea (*Chamaecrista fasciculata*) mix at rates of 11.2 and 3.4 kg/ha, respectively. Severe drought during the 2000 growing season resulted in poor plant growth; therefore, field borders were re-seeded in early 2001. Despite these two attempts to establish field borders, most re-seeded naturally from seed present within the seed bank. During the 2001 growing season, the most common species occurring in field borders were morning-glory (*Ipomoea* spp.), crabgrass (*Digitaria ciliaris*), Johnson grass, hemp sesbania (*Sesbania exaltata*), yellow nutsedge (*Cyperus esculentus*), and ragweed (*Ambrosia* spp.; PJB unpubl. data).

*Data collection.*—We used line-transect distance sampling and strip-transect sampling to estimate density (birds/ha) and diversity, respectively, of wintering grassland birds. Georeferenced aerial photos and Geographic Information System (GIS) land cover maps were used to delineate field edges. Field edges were divided into 200-m-long sampling units (transects), with the beginning point of each transect situated so that the vegetation type on the non-agricultural side of the transect was homogeneous for the length of the transect. The centerline of each transect was situated along the interface of the original (before field borders implemented) row-crop field and adjacent plant community interface. Transects located adjacent to roadways or those that contained field borders that were disturbed inadvertently (e.g., disked, mowed, sprayed) by producers were not included within this sampling frame. Our sampling frame consisted of 110 bordered and 82 non-bordered transects. We then classified each transect based upon combinations of (1) bordered (T) and non-bordered (C) practices on the agricultural side, and by (2) vegetation type (woody [W], herbaceous [G]) and (3) width (strip [S],  $\leq 30$  m of continuous vegetation type; block [B],  $> 30$  m of contin-

uous vegetation type) on the non-agricultural side. This classification scheme produced eight treatment combinations: TGB, CGB, TGS, CGS, TWB, CWB, TWS, CWS.

During winter 2002, we conducted a pilot study to estimate encounter rates along potential transects within each treatment combination. We concluded that  $\geq 10$  200-m transects/treatment combination would provide sufficient numbers of encounters to estimate detection functions for several common species and most guilds. Because the amount and structure of grassland and woodland habitats differed dramatically among farms, we were not able to sample all eight treatment combinations within any one farm. Therefore, we randomly selected 10–11 transects for each treatment combination from the population of transects available across all three farms except for the CGB treatment combination. Only seven transects were available for the CGB treatment combination and all were used. We sampled the same transects in both years of study (2002, 2003), with the exception of two TWB transects with field borders that were accidentally disked by the producer after year 1. These two transects were replaced by two other randomly selected TWB transects on the same farm.

The field border treatment was assigned randomly to one-half of each of the three farms. Field borders were not assigned randomly to individual transects, but rather bordered transects were selected randomly from the population of all bordered transects across all farms. Thus, our study was observational with replication. Additionally, distance sampling assumes implicitly that transects are placed randomly relative to the distribution of objects (birds) within a study area for justifiable extrapolation of sample statistics to the population (Buckland et al. 2001). Our objectives were not to estimate study area density, but rather densities of birds inhabiting or using designated portions (field borders and adjacent communities) of a study area.

We marked transects with flagging at the beginning, end, and at 20-m intervals along each transect to allow observers to monitor their rate of speed and location during the surveys. Sampling was conducted by two observers each year. Within each sampling interval, we randomly assigned transects to an observ-

er; within each farm, however, we sampled transects in a systematic order to reduce travel time between transects. Each observer sampled 3–8 transects/morning/farm. Transect order within each farm was alternated among repetitions (i.e., transects were sampled in reverse order during the second repetition). Moreover, following completion of the first repetition, observers switched transect schedules. We sampled all transects three times in 2002 and twice in 2003 during February–March, with approximately 3–4 weeks between visits to the same transect (Freemark and Rogers 1995).

We walked at approximately 20 m/min along each transect and made intermittent stops to record the number of individuals and species seen or heard on each side of the transect line. Transects were sampled between 07:00 and 10:00 (CST) with wind speeds <16 km/hr. We assigned observations into one of four perpendicular distance bands (0.0–9.9, 10.0–19.9, 20.0–29.9, and >30.0 m) on each side of the transect line. The first distance band in bordered transects contained the field border, whereas the first distance band for non-bordered transects was the first 9.9 m of crop field. To reduce observer bias, additional observers ( $n = 2$ ) were trained by PJB and SJD prior to sampling (Kepler and Scott 1981, Smith 1984). Each observer was trained in sampling protocol, bird identification (by sight and sound), and distance estimation (Scott et al. 1981). Furthermore, we assumed that observers were able to detect all birds on the transect line, detect birds at their initial location, and assign observations to correct distance categories (Buckland et al. 2001). PJB collected data during both years of the study, whereas each of the additional observers collected data for only 1 year.

**Density estimation.**—Because avian detection probabilities (Bibby and Buckland 1987, Buckland et al. 2001) and assemblages (Best 1983, Shalaway 1985, Best et al. 1990, Sparks et al. 1996) differ with plant community structure and composition, we decided *a priori* to develop independent detection functions for the agricultural and non-agricultural sides of transects. On the agricultural side, we developed detection functions for bordered (T) and non-bordered (C) transects. We also stratified the non-agricultural side of transects based on

vegetation type (W, G) and width (S, B). Thus, we developed six detection functions (T, C, GS, GB, WS, WB) for each species or guild. We tested pooling robustness (Burnham et al. 1980, Buckland et al. 2001) of the six functions by comparing Akaike's Information Criterion (AIC; Akaike 1974) values between distance data fitted to pooled (e.g., using all observations on the non-agricultural side of wooded transects) and unpooled functions (e.g., wood strip and wood block observations on the non-agricultural side of wooded transects). When comparing functions from the same set of data, a greater AIC value of a pooled model—relative to the sum of AIC values of the unpooled models—indicates that individual models fit the data better than a pooled model (Buckland et al. 2001). Testing of model robustness was conducted only between models on the agriculture sides of transects (T, C) and between models within vegetation types on the non-agricultural sides of each transect (i.e., wood block and wood strip within woods). We assumed that detection functions did not differ between or within years; thus, we pooled observations across years and repetitions. Although some species occasionally occurred in loose aggregations, we treated all individuals as unique, independent observations.

We used Program DISTANCE (Thomas et al. 1998) to model detection functions for species and guilds for which we recorded >60 observations within each of the six habitat types (Buckland et al. 2001). Only Song (*Melospiza melodia*) and Savannah (*Passerculus sandwichensis*) sparrows were detected often enough within these six habitat types to develop species-specific detection functions. We also developed detection functions for an "other sparrows" group (hereafter other sparrow) by pooling observations of Swamp Sparrow (*Melospiza georgiana*;  $n = 364$ ), Northern Cardinal (*Cardinalis cardinalis*;  $n = 306$ ), White-throated Sparrow (*Zonotrichia albicollis*;  $n = 147$ ), unidentified sparrow ( $n = 106$ ), Eastern Towhee (*Pipilo erythrophthalmus*;  $n = 104$ ), Field Sparrow (*Spizella pusilla*;  $n = 27$ ), Vesper Sparrow (*Pooecetes gramineus*;  $n = 16$ ), Fox Sparrow (*Passerella iliaca*;  $n = 14$ ), White-crowned Sparrow (*Zonotrichia leucophrys*;  $n = 12$ ), Chipping Sparrow (*Spizella passerina*;  $n = 6$ ), and Lark Sparrow

(*Chondestes grammacus*;  $n = 2$ ). Because these species have somewhat similar foraging strategies during winter (i.e., granivorous ground-feeding birds that forage close to cover; Bent 1968), we assumed that detection probabilities were similar among species and could be modeled with a common detection function.

Prior to analyses, we visually inspected the data by plotting observations by distance band for each detection function. The half-normal base function, with cosine or hermite polynomial adjustment terms, and the hazard-rate base function, with either cosine or polynomial adjustment terms, were selected as likely base-function, adjustment-term combinations that would best model the data. Base functions and series expansion terms, increasing in complexity (number of estimatable parameters), were sequentially evaluated by comparing AIC values among competing models (Burnham and Anderson 1998, Anderson et al. 2000). When a more complex model failed to adequately fit the data relative to the number of parameters within the model (greater AIC), the previous model was selected as the best approximating model. Right truncation was set to 65 m, equal to the midpoint between the beginning of the last distance band ( $>30$  m) and 100 m.

We estimated bird density independently for the agricultural and non-agricultural sides of the transect. We used the T and C detection probabilities (value of probability density function  $f_{(x)}$  evaluated at 0) to compute densities for the agricultural side of all bordered and non-bordered transects, respectively. These two density estimates (bordered and non-bordered on the agricultural side) represented the effect of field borders without accounting for birds inhabiting the adjacent plant community. On the non-agricultural side, we used the GB, GS, WB, and WS detection probabilities to estimate densities using only respective transects that had either a field border or no field border on the agricultural side. We then combined these class-specific density estimates to estimate the joint density for a field edge with a given combination of adjacent plant community and border type. For example, we combined the density estimates for the herbaceous block (GB), non-agricultural side of bordered transects

with the density estimate of bordered transects (T) on the agricultural side to produce the density estimate for the TGB treatment combination. We believe this approach best accommodates instances where detection functions differ between sides of the same transect line. All reported densities and variances were generated using 1,000 bootstrap samples (with replacement) incorporating detection probabilities and numbers of observations/transect/treatment combination (Buckland et al. 2001). We used a Z-test to evaluate border effects between like pairs (e.g., CGB versus TGB) (Buckland et al. 2001). All results were considered significant at  $\alpha = 0.05$ .

*Community structure.*—To characterize community structure and relative conservation value of bordered and non-bordered field edges, we calculated species richness, the Shannon-Weaver diversity index (Shannon and Weaver 1949), and total avian conservation value (TACV; Nuttle et al. 2003) using only observations within the first distance interval on each side of the transect centerline. TACV is a weighted index of community conservation value calculated by multiplying species-specific abundances by their respective Partners in Flight (PIF) conservation priority scores (Carter et al. 2000). Species-specific scores were summed across all species within a given transect to produce a transect TACV score. PIF priority scores reflect different degrees of need for conservation attention based on breeding and wintering distributions, relative abundance, potential threats to breeding and wintering habitats, population trend, and a physiographically specific value of area importance (Carter et al. 2000). We used PIF priority scores for species that winter in the East Gulf Coastal Plain physiographic region. "Fly-overs" were not included. We used  $t$ -tests to determine differences in mean species richness, Shannon Diversity, and TACV between bordered and non-bordered transects by adjacent plant community. Where unequal variances occurred, we used Satterthwaite's adjusted degrees of freedom (Milliken and Johnson 1992). All results were considered significant at  $\alpha = 0.05$ .

## RESULTS

We recorded 71 species and 17,562 individual birds while sampling 155.2 km of tran-

TABLE 1. Sampling effort and model selection of detection functions of wintering Song, Savannah, and other sparrows along bordered and non-bordered agricultural field edges in Clay and Lowndes counties, Mississippi, 2002–2003.

Species/Class	$n^a$	$L^b$	$n^c$	Model selected	$f_{(0)}$	$m^d$	AIC
Song Sparrow							
Border	317	40,000	44	HN <sup>e</sup> + cosine	0.2353	1	15.52
Non-border	76	37,600	38	HN + cosine	0.0940	1	95.63
Pooled Ag. <sup>f</sup>	393	77,600	82	HR + cosine	0.1353	2	163.86
Grass block	187	17,000	17	HR <sup>g</sup> + cosine	0.0890	2	236.66
Grass strip	240	20,600	22	HR + polynomial	0.6189	3	178.82
Pooled grass <sup>f</sup>	427	37,600	39	HN + cosine	0.1332	3	421.99
Wood block	250	20,000	22	HN + cosine	0.1316	1	165.40
Wood strip	137	20,000	21	HR + cosine	0.2025	2	100.31
Pooled wood <sup>f</sup>	387	40,000	43	HR + cosine	0.1453	2	269.64
Savannah Sparrow							
Border	151	40,000	44	HN + cosine	0.1435	1	80.91
Non-border	210	37,600	38	HR + polynomial	0.0350	2	528.49
Pooled Ag. <sup>f</sup>	361	77,600	82	HR + polynomial	0.1045	3	744.35
Grass block	82	17,000	17	HR + cosine	0.1396	2	67.37
Grass strip	463	20,600	22	HN + cosine	0.1331	1	298.10
Pooled grass <sup>f</sup>	545	37,600	39	HN + cosine	0.1300	1	369.13
Wood block	5	20,000	22	HN + cosine	0.0813	1	9.50
Wood strip	98	20,000	21	HN + cosine	0.1632	1	35.43
Pooled wood <sup>f</sup>	103	40,000	43	HN + cosine	0.1513	1	47.79
Other sparrows							
Border	186	40,000	44	HR + cosine	0.8448	2	73.49
Non-border	49	37,600	38	HR + cosine	0.0251	2	139.89
Pooled Ag. <sup>f</sup>	235	77,600	82	HR + cosine	0.6150	3	323.82
Grass block	145	17,000	17	HR + cosine	0.3594	2	282.15
Grass strip	215	20,600	22	HR + cosine	0.6039	3	346.38
Pooled grass <sup>f</sup>	360	37,600	39	HR + cosine	0.5463	3	629.09
Wood block	276	20,000	22	HN + cosine	0.0885	3	537.16
Wood strip	287	20,000	21	HR + cosine	0.6893	3	380.04
Pooled wood <sup>f</sup>	563	40,000	43	HN + cosine	0.0981	3	937.29

<sup>a</sup> Number of observations.

<sup>b</sup> Sampling effort (total length of transects in meters).

<sup>c</sup> Number of transects.

<sup>d</sup> Number of parameters in detection function.

<sup>e</sup> Half-normal base function.

<sup>f</sup> Pooled detection functions were not used to compute density.

<sup>g</sup> Hazard-rate base function.

sects during 2002–2003. The five most abundant species were Red-winged Blackbird (*Agelaius phoeniceus*; 44.7%), American Pipit (*Anthus rubescens*; 11.2%), Song Sparrow (6.9%), Savannah Sparrow (5.7%), and American Robin (*Turdus migratorius*; 4.9%). Detection functions for Song, Savannah, and other sparrows were not robust to pooling across adjacent plant communities (Table 1); therefore, we used detection functions specific to the adjacent plant community to compute density estimates for each species.

**Density.**—Song Sparrow densities (birds/ha) differed between bordered and non-bor-

dered field edges adjacent to grass block (border = 30.86, SE = 4.19; non-border = 8.29, SE = 2.58;  $Z = 4.59$ ,  $P < 0.001$ ) and wooded strip ( $P < 0.001$ ) plant communities (Table 2). However, no difference in Song Sparrow density was observed between bordered and non-bordered transects adjacent to herbaceous strips ( $P = 0.24$ ) and wooded blocks ( $P = 0.35$ ; Table 2). Savannah Sparrow densities did not differ between bordered and non-bordered transects adjacent to herbaceous blocks (border = 14.95, SE = 6.14; non-border = 4.74, SE = 1.45;  $Z = 1.62$ ,  $P = 0.053$ ), herbaceous strips ( $P = 0.13$ ), wooded blocks ( $P$

TABLE 2. Mean wintering densities (birds/ha) of Song, Savannah, and other sparrows along bordered and non-bordered agricultural field edges by adjacent plant community in Clay and Lowndes counties, Mississippi, 2002–2003.

Species/ Adjacent plant community <sup>a</sup>	Bordered <sup>b</sup>		Non-bordered		RES <sup>c</sup>	Z-test	P-value
	Mean	SE	Mean	SE			
Song Sparrow							
Grass block	30.86	4.19	8.29	2.58	272.25	4.59	<0.001
Grass strip	95.87	30.00	70.03	20.90	36.90	0.71	0.24
Wood block	25.34	3.68	28.20	6.38	-10.14	-0.39	0.35
Wood strip	38.17	4.92	10.24	2.18	272.75	5.20	<0.001
Savannah Sparrow							
Grass block	14.95	6.14	4.74	1.45	215.40	1.62	0.053
Grass strip	18.05	9.93	47.51	24.27	-62.01	-1.12	0.13
Wood block	5.40	2.44	2.35	1.23	129.78	1.12	0.13
Wood strip	21.47	15.08	2.28	1.24	841.67	1.27	0.10
Other sparrows							
Grass block	78.20	12.99	19.36	7.96	303.93	3.86	<0.001
Grass strip	138.98	18.05	30.01	7.39	363.11	5.59	<0.001
Wood block	51.44	11.81	12.55	2.70	309.88	3.21	<0.001
Wood strip	128.94	16.98	107.69	26.80	19.73	0.67	0.25

<sup>a</sup> Adjacent plant community on the non-agriculture side of the transect.

<sup>b</sup> Mean is the sum of densities of agricultural and non-agricultural sides of transects.

<sup>c</sup> Relative effect size:  $((\text{border} - \text{non-border})/\text{non-border}) \times 100$ .

= 0.13), and wooded strips ( $P = 0.10$ ; Table 2).

Other sparrow densities differed with respect to bordered and non-bordered transects along herbaceous block (border = 78.20, SE = 12.99; non-border = 19.36, SE = 7.96;  $Z = 3.86$ ,  $P < 0.001$ ), herbaceous strip ( $P < 0.001$ ), and wooded block ( $P < 0.001$ ) communities (Table 2). However, densities did not differ along wooded strips ( $P = 0.25$ ; Table 2). Most Field Sparrow (92.6%) and Swamp Sparrow (91.8%) observations occurred along bordered transects. We recorded similar numbers of Northern Cardinal (border = 145; non-border = 161), Eastern Towhee (border = 44; non-border = 60), Chipping Sparrow (border = 3; non-border = 3), White-throated Sparrow (border = 62; non-border = 85), Vesper Sparrow (border = 7; non-border = 9), and unidentified sparrows (border = 103; non-border = 56) along bordered and non-bordered transects; however, few Fox Sparrows (border = 1; non-border = 13) and no White-crowned or Lark sparrows were recorded along bordered transects.

**Community structure.**—We recorded 59 species (6,108 individuals) within one distance band on each side of transects. The most

abundant species were Song Sparrow (22.7%), American Robin (7.5%), Savannah Sparrow (6.9%), Swamp Sparrow (6.8%), and Northern Cardinal (6.8%). Species richness, diversity, and TACV did not differ between bordered and non-bordered transects, regardless of the adjacent plant community type (Table 3).

## DISCUSSION

Brennan (1991), Rodenhouse et al. (1993), and Warner (1994) suggested that the elimination of grassy edge communities around agricultural field edges and fencerow habitats contributed to the decline of Northern Bobwhite (*Colinus virginianus*) and many other grassland species inhabiting farmlands. Most sparrows are ground foragers (Wheelwright and Rising 1993, Arcese et al. 2002) and their use of strip-cover habitats often depends upon vegetation structure (Bryan and Best 1991, Rodenhouse et al. 1993, Camp and Best 1994). We observed greater densities of several sparrow species where field borders were established. However, this effect varied by species and type of adjacent plant community. Song Sparrow and other sparrow densities were greatest where field borders were established along existing grasslands. The habitat

TABLE 3. Species richness, Shannon-Weaver diversity index, and total avian conservation value using observations within one distance-band on each side of transects along bordered and non-bordered agricultural field edges by adjacent plant community type in Clay and Lowndes counties, Mississippi, 2002–2003.

Measure/ Adjacent plant community <sup>a</sup>	Bordered		Non-bordered		RES <sup>b</sup>	t-test	P-value
	Mean	SE	Mean	SE			
<b>Species richness</b>							
Grass block	6.60	0.22	5.29	0.78	24.76	1.62	0.15
Grass strip	6.54	0.79	8.00	0.96	-18.25	-1.17	0.26
Wood block	7.00	1.16	9.30	1.42	-24.73	-1.27	0.22
Wood strip	10.18	1.16	11.50	1.12	-11.48	-0.82	0.43
<b>Shannon-Weaver</b>							
Grass block	1.37	0.08	1.28	0.14	7.03	0.58	0.57
Grass strip	1.21	0.09	1.42	0.15	-14.79	-1.20	0.24
Wood block	1.29	0.17	1.35	0.15	-4.44	-0.24	0.81
Wood strip	1.60	0.19	1.92	0.20	-16.67	-1.19	0.25
<b>Total avian conservation value</b>							
Grass block	970.60	145.05	566.00	157.00	71.48	1.86	0.08
Grass strip	1,199.55	272.22	1,403.00	409.61	-14.50	-0.41	0.68
Wood block	677.67	191.01	996.70	273.72	-29.00	-0.98	0.34
Wood strip	2,421.18	1,392.05	694.30	96.97	248.72	1.24	0.24

<sup>a</sup> Adjacent plant community on the non-agricultural side of the transect.

<sup>b</sup> Relative effect size:  $((\text{border} - \text{non border})/\text{non-border}) \times 100$ .

value of herbaceous field borders adjacent to grasslands may seem paradoxical, but most grasslands on our study farms were monotypic stands of cool-season, exotic forage grasses that provided little vertical structure and little seed-production. Only Song Sparrow densities were greater along wooded strip habitats with a field border. Once crops were harvested, field border habitats provided the structural vegetation characteristics commensurate with the foraging ecology of most sparrows. Field borders were recently established (<3 years old) and consisted primarily of seed-producing grasses and forbs coupled with a relatively open understory that facilitated ground-based foraging. Additionally, field borders provided escape cover in close proximity to other foraging sites, mainly row-crop fields containing waste grain. Therefore, we speculate that field borders may enhance the value of existing grasslands and cropland by producing additional foraging habitat and escape cover in close proximity to waste-grain food sources. The net effect of field borders may be to increase usable space and carrying capacity for sparrows in agricultural landscapes.

Given that most sparrow species observed in our study had somewhat similar foraging strategies, we had expected field borders to

elicit similar responses across most sparrow species. With the exception of Song, Field, and Swamp sparrows, Savannah Sparrows and five of the other sparrow species were equally abundant along bordered and non-bordered transects, regardless of adjacent plant community. Whereas our estimates for other sparrows were markedly different between bordered and non-bordered transects across all of the adjacent plant communities (except for wooded strips), this effect was heavily weighted by observations of Swamp Sparrows. Swamp Sparrows were most strongly associated with bordered transects and composed a large proportion (31.5%) of other sparrow observations. Thus, our observed border effects for other sparrows were attributable mainly to greater densities of Swamp Sparrows along bordered transects. Collectively, across most adjacent plant communities, we observed greater densities of Song, Field, and Swamp sparrows along bordered transects. Responses of other sparrow species were either equivocal or negative. Overall, field borders apparently elicited greater use from only a few selected species in our study. The effect of field borders on other species or communities in other physiographic regions remains unknown.

*Conservation implications.*—Field borders

may provide important habitat in southern agricultural systems where many eastern grassland species of short-distance migrants overwinter. Murphy (2003) reported strong associations between changes in farmland structure and population trends of short-distance migrant grassland birds and suggested that this association existed because short-distance migrants were affected by changes in agricultural landscapes during both the breeding and wintering seasons. The value of strip habitats has been a source of debate regarding their ability to serve as population sources during the breeding season; however, their roles during the wintering period are unknown. The availability of food resources during winter has been shown to enhance survival and body condition of birds (Porter et al. 1980, Brittingham and Temple 1988, Desrochers et al. 1988, Egan and Brittingham 1994). Although the survivorship of birds wintering in strip habitats is not known, we contend that the annual grasses characteristic of these idle communities might provide important thermal and energetic resources (Klute et al. 1997, Best et al. 1998).

Weed seeds are the primary energy source for most wintering sparrows (Wheelwright and Rising 1993, Mowbray 1997, Arcese et al. 2002). We recommend that field borders be maintained in early seral stages through periodic disturbance (e.g., fire or disking) to provide greater quantities of, and accessibility to, seeds of annual plants during the winter (Burger et al. 1990, Millenbah et al. 1996, Best et al. 1998, Greenfield et al. 2002). Seral species, such as giant ragweed, provide comparatively high levels of metabolizable energy relative to other non-agriculture plant seeds (Robel et al. 1979). Additionally, field borders may provide safe access to other highly metabolizable food sources, such as waste grain. Collectively, we suggest that field borders provide important winter habitat for many grassland birds due to their greater abundance of food (weed seed) and more complex vegetation structure for roosting, loafing, thermal, and escape cover than that found in adjacent row crops and grasslands.

Identifying resource management systems that support both birds and farm operators is important for maintaining a diverse farmland avifauna (Rodenhouse et al. 1993, Musters et

al. 2001, Murphy 2003). Environmental benefits (e.g., decreased runoff of herbicides and nutrients, reduced soil erosion and sedimentation) of field-border conservation practices are well documented; the wildlife habitat value of field borders, especially during winter, is not as well understood. Our results suggest that field borders support greater densities of certain sparrow species along agricultural field edges during the winter, but they may not necessarily support greater species richness and diversity. These results, combined with our current understanding of environmental and economic benefits of field borders, suggest that field-border conservation practices are compatible with the needs of farm operators while diversifying farmland vegetation structure to enhance local avifauna.

The U.S. Department of Agriculture's National Conservation Buffer Initiative practices, such as field borders, offer potential opportunities for enhancing wintering habitat for numerous grassland birds on southeastern farmlands. Widespread implementation of field-border conservation practices is currently feasible (through Farm Bill programs) and likely to occur given the growing public concern regarding sustainable agriculture. However, as noted by Peterjohn (2003), simple, all-encompassing solutions will not reverse significant declines of farmland birds; field-border conservation practices may only benefit some species in some physiographic regions. We agree with Herkert et al. (1996) and Peterjohn (2003) in their assertion that the greatest gap in our knowledge of farmland bird ecology is winter ecology. We recommend that a greater emphasis be placed on research addressing overwinter benefits of farmland conservation practices to wildlife.

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## COMPOSITION, ABUNDANCE, AND TIMING OF POST-BREEDING MIGRANT LANDBIRDS AT YAKUTAT, ALASKA

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**ABSTRACT.**—The eastern Gulf of Alaska coastline is suspected of providing an important pathway for birds migrating to and from Alaska. Because no intensive study of landbird migration has been conducted in this region, we used mist nets to study the post-breeding migration of landbirds along the coast from 1994 through 1999. Over six post-breeding periods, we netted for a total of 316 days (23,538 net-hr) and captured 13,490 individuals of 46 species (57.3 birds/100 net-hr). Six species constituted >65% of all captures (ordered by abundance): Orange-crowned Warbler (*Vermivora celata*), Hermit Thrush (*Catharus guttatus*), Lincoln's Sparrow (*Melospiza lincolni*), Ruby-crowned Kinglet (*Regulus calendula*), Fox Sparrow (*Passerella iliaca*), and Yellow Warbler (*Dendroica petechia*). Most birds captured (71%) were Nearctic-Neotropical migrants, and percentages of hatching-year (HY) birds varied from 51 to 90% among common species. Daily capture rates of all species were highest between mid-August and mid-September. Migration of HY individuals preceded that of after-hatching-year (AHY) birds in 70% of the Nearctic-Neotropical species. Masses of HY Nearctic-Neotropical migrants were significantly less than those of AHY individuals. High capture rates and consistent annual use indicate that the eastern Gulf of Alaska coast is an important pathway for many small landbird migrants, particularly Nearctic-Neotropical species, departing breeding grounds in southern Alaska. Received 5 April 2004, accepted 23 May 2005.

Birds are subjected to many physical and behavioral challenges when they migrate. Because of the costs associated with undertaking these twice-annual movements, how birds respond to migration challenges has a profound effect on their population dynamics. Despite the critical role migration plays in their annual life cycles, knowledge about the migration biology and ecology of many birds, particularly of small landbirds, remains only rudimentary throughout North America (Moore et al. 1995, Hutto 1998, Moore 2000). Information on small landbird migration in northern North America is particularly depauperate; relatively few studies of the migration of small landbirds have been conducted anywhere in Alaska (but see Bailey 1974, Manuwal and Manuwal 1979, Gibson 1981, Cooper and Ritchie 1995, Benson and Winker 2001).

Isleib and Kessel (1973) suggested that the

eastern Gulf of Alaska coastline is an important pathway for landbirds migrating to and from Alaska. Although some waterfowl species initiate spring over-water crossings of the Gulf of Alaska from the coast of the western United States and Canada, radar observations confirm that most birds migrate within a 20-km band offshore of British Columbia and southeastern Alaska (Myres 1972). The close proximity of tall (>3,000 m) mountains to the coast probably restricts inland passage of migrants; however, major river systems that bisect coastal mountains likely funnel some coastal migrants into and out of breeding grounds in interior Alaska, Yukon, and British Columbia (Isleib and Kessel 1973, Patten 1982). Although the migration of shorebirds, waterfowl, and raptors in the region has been somewhat studied (e.g., Patten 1982, Swem 1983, Andres and Browne 1998), virtually no information exists that describes migration patterns of small landbirds. Therefore, we undertook a study to determine the species and age composition, abundance, and timing of post-breeding, small landbirds that migrate along the eastern Gulf of Alaska coastline.

### METHODS

The Yakutat Foreland (Foreland) is located along the Pacific coast of Alaska and extends 140 km southwesterly from the town of Yakutat (59° 30' N, 139° 50' W) to Cape Fair-

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TABLE 1. Effort and captures during mist netting of post-breeding landbird migrants at Yakutat, Alaska, 1994–1999.

Year	Number of nets	Days (%) <sup>a</sup>	Total net-hr	Birds captured	Capture rate <sup>b</sup>
1994	10	87	3,217	2,217	68.9
1995	11	78	3,306	1,359	41.1
1996	13	80	3,593	1,962	54.6
1997	13	85	4,215	2,122	50.3
1998	15	88	4,565	3,225	70.6
1999	15	83	4,642	2,605	56.1
All years		83	23,538	13,490	57.3

<sup>a</sup> Percentage of possible days (1994 = 54 days, 1995–1999 = 65 days) nets were operated.

<sup>b</sup> Birds/100 net-hr.

weather (58° 48' N, 138° 00' W). This glacial plain varies in width from 30 to 70 km and is bounded on the east by the St. Elias Mountains and Brabazon Range and on the west by the Gulf of Alaska. The Foreland is characterized by sandy beaches, extensive sand dunes, tidal mudflats, deciduous shrublands, spruce forests, and muskegs and is transected by a series of relatively short, mostly clear-running rivers (Patten 1982). Most of the area is administered by the U.S. Forest Service as part of the Tongass National Forest.

We established a banding station 1.6 km west of the Yakutat airport (59° 30' N, 139° 40' W). The site was primarily open (65%) and vegetated by bryophytes, grasses, sedges, forbs, and sweetgale (*Myrica gale*); patches of willows (*Salix* spp.) and solitary Sitka spruces (*Picea sitchensis*) were interspersed throughout. A dense perimeter of Sitka spruce, alder (*Alnus* spp.), willow, and ferns bounded two sides of the study area.

Post-breeding landbirds were captured in mist nets. Initially, 10 nets (12 × 2.6 m, 30-mm mesh) were erected and placed at ~50-m intervals; additional nets were added in subsequent years (Table 1). Most nets were placed in scattered shrub patches, and a few were set in the dense perimeter of spruce and alders. Overall, our mist nets sampled a total area of about 7.5 ha. From 1 August to 4 October (except for 1994 when we ended netting on 23 September), nets were opened daily at sunrise (with a minimum starting time of 04:30 AST) and operated for an average of 6 (1995–1999) or 7 hr (1994). Nets were operated in intermittent and light rain, but not in

heavy rain or when wind was >26 km/hr. Netting ended by 14:00 and was not initiated on days when weather delayed opening the nets until after 11:00. Two to four trained observers checked nets at 30-min intervals. Captured birds were removed and transported to a central processing station where standard morphological data, as described by Ralph et al. (1993), were collected. Age was determined primarily by degree of skull ossification and secondarily by diagnostic plumage characteristics; all species could be reliably aged if skull pneumaticization was incomplete (Pyle et al. 1987, Pyle 1997). To facilitate rapid processing on high capture days, we sometimes only recorded age and sex. We used available morphological descriptions (metrics and plumage) to determine whether migrants originated from coastal or interior Alaska populations (Gabrielson and Lincoln 1959, Pyle et al. 1987, Gibson and Kessel 1997, Pyle 1997). Overall mist-net mortality was <0.3%; most deaths were attributable to inclement weather or predation by mink (*Mustela vison*), ermine (*Mustela erminea*), or red squirrels (*Tamiasciurus hudsonicus*).

Our analysis was restricted to landbird species within the Apodiformes, Piciformes, and Passeriformes. Nomenclature follows the American Ornithologists' Union (1998) check-list and subsequent supplements. Total numbers, capture rates (birds/100 net-hr), and proportions of all captures were calculated for each species across all years. The coefficient of variation (CV = 100 × SD/mean) of annual capture rates (1995–1999, when capture periods were similar) was used to assess between-year variation. We included handled birds that escaped before banding in calculating overall capture rates but excluded captured individuals that were previously banded. To assess occurrence of species not sampled by mist nets, we kept a daily record of all species observed while mist netting. Lastly, we categorized species, according to migration distance, as Nearctic–Neotropical migrants, Nearctic–Nearctic migrants, or residents.

We calculated the proportion of hatching-year (HY) individuals captured for species where >30 individuals were aged. We determined species-specific median passage dates for all HY, after-hatching-year (AHY), and total individuals, and the ranges of dates that

included 90% of captures of all ages. Due to the large numbers of individuals that occurred on the same dates, we used a chi-square statistic, corrected for continuity, to test for age-related differences in passage timing by comparing the number of individuals in each age-class that fell above and below the median passage date for each species. We used a *t*-test, with Satterthwaite's approximation of degrees of freedom (Snedecor and Cochran 1980:97), to compare median passage dates of Nearctic-Neotropical species and Nearctic-Nearctic species and to compare mean mass between HY and AHY birds. Lastly, we used weighted least-squares regression to evaluate the relationship between mass ratios (HY:AHY; response variable) and migration-distance categories (Nearctic-Neotropical > Nearctic-Nearctic > resident).

## RESULTS

From 1994 through 1999, we captured 13,490 individuals of 46 landbird species (57.3 birds/100 net-hr). An additional 11 species were observed but not captured. Annual capture rates varied between 41.1 and 70.6 birds/100 net-hr (Table 1). Kinglets, Hermit Thrushes, wood-warblers, and sparrows were most frequently captured, whereas corvids, woodpeckers, American Robins, Varied Thrushes, and finches were observed more often than captured (Table 2, Appendix). Six species individually represented  $\geq 5\%$  of all birds captured and together constituted 65% of the all captures (Table 2). Several species (Steller's Jays, Common Ravens, Chestnut-backed Chickadees, Golden-crowned Kinglets, American Robins, and Varied Thrushes) were recorded on a high percentage of days, but they may have represented repeated observations of locally breeding individuals or residents rather than new observations of passage migrants (Table 2). For 40% of the species encountered, either we captured <10 individuals or they were observed on <10% of the mist-netting days (Appendix).

Twenty-seven species that were observed or captured, and 71% of all captures, were Nearctic-Neotropical migrants ( $n = 23$  species). Another 17 species were Nearctic-Nearctic migrants (18% of all captures,  $n = 13$  species), and 13 species (11% of all captures,  $n = 11$  species) were resident. Coefficients of

variation (CV) of annual capture rates for regularly occurring species were generally <50% (Table 2). Red-breasted Nuthatches were captured only in 1994 but were observed in moderate numbers other years. Sixty-two percent of all fringillids were captured in a single year (1998), and these species—known to be irruptive—had some of the highest CVs for inter-annual capture rates (Table 2).

Where readily discernible, morphometric measurements and plumage characteristics indicated that migrants captured at Yakutat originated from coastal Alaskan populations (Hermit Thrush, Orange-crowned Warbler, Fox Sparrow, and Song Sparrow). Four recaptures linked Yakutat to other locations along the Pacific coast: (1) a Yellow-rumped Warbler recaptured at Redding, California; (2) a Song Sparrow re-sighted at Juneau, Alaska; (3) a Fox Sparrow recaptured at Long Beach, Washington; and (4) a Golden-crowned Sparrow banded at Niles, California and recaptured at Yakutat. Additionally, the only Sharpshinned Hawk (*Accipiter striatus*) we banded in 6 years was recaptured outside of Vancouver, British Columbia, and a Yellow Warbler banded on the Alaska Peninsula was recovered 4 days later on a fishing boat 17 km off Yakutat's coast.

Hatching-year birds dominated captures of most species (Table 2), and proportionally fewer young warblers (65%) were captured than were young sparrows (81%;  $\chi^2 = 228$ ,  $df = 1$ ,  $P < 0.001$ ). No consistent patterns of HY captures were evident among species of different migration-distance categories; high (>90%) percentages of young were captured in some species of residents, Nearctic-Nearctic migrants, and Nearctic-Neotropical migrants. Of the 15 rarest Nearctic-Neotropical and Nearctic-Nearctic migrants, the combined percentage of HY birds (91.2%,  $n = 91$  individuals) exceeded that of any individual, common species. The high percentage of adult White-winged Crossbills captured in September 1998 was attributable to their concurrent nesting activity at the site.

Daily capture rates of many small landbird migrants were highest between mid-August and mid-September. However, specific timing differed among species (Table 3). Median passage date of Nearctic-Neotropical migrant species was 12–13 days earlier than it was for

TABLE 2. Abundance of post-breeding, small landbirds commonly caught in mist nets or observed at Yakutat, Alaska, 1994–1999. Coefficient of variation (CV) calculated as  $SD \times 100/\text{mean}$  for species with >10 total captures. Species ordered by migration-distance category.

Species	Total captures <sup>a</sup>	% days observed <sup>a</sup>	Birds/100 net-hr <sup>b</sup>			Hatching-year <sup>b</sup>	
			All years	% of total	CV (%)	%	n <sup>c</sup>
<b>Nearctic-Neotropical migrants</b>							
Alder Flycatcher ( <i>Empidonax alnorum</i> )	50	6	0.21	0.4	81	76	42
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	1,069	80	4.20	7.5	42	83	823
Hermit Thrush ( <i>Catharus guttatus</i> )	2,016	69	8.37	15.0	28	85	1,679
American Robin ( <i>Turdus migratorius</i> )	12	63	0.05	0.1	134	— <sup>d</sup>	— <sup>d</sup>
Orange-crowned Warbler ( <i>Vermivora celata</i> )	2,128	67	9.17	16.4	13	61	1,815
Yellow Warbler ( <i>Dendroica petechia</i> )	803	29	3.26	5.8	51	66	651
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	456	42	1.95	3.5	79	86	388
Townsend's Warbler ( <i>Dendroica townsendi</i> )	16	2	0.06	0.1	53	—	—
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	559	31	2.26	4.0	70	77	449
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	529	37	2.25	4.0	38	67	448
Lincoln's Sparrow ( <i>Melospiza lincolni</i> )	1,871	67	7.48	13.4	36	89	1,453
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	86	10	0.37	0.7	54	96	75
<b>Nearctic-Nearctic migrants</b>							
Northern Flicker ( <i>Colaptes auratus</i> )		13					
Red-breasted Nuthatch <sup>e</sup> ( <i>Sitta canadensis</i> )	81	43	0.33	0.6	245	72	65
Brown Creeper ( <i>Certhia americana</i> )	26	9	0.07	0.1	59	—	—
Winter Wren ( <i>Troglodytes troglodytes</i> )	97	23	0.35	0.6	27	62	84
Varied Thrush ( <i>Ixoreus naevius</i> )	106	79	0.40	0.7	40	80	81
American Tree Sparrow ( <i>Spizella arborea</i> )	25	1	0.12	0.2	103	—	—
Fox Sparrow ( <i>Passerella iliaca</i> )	898	40	4.05	7.3	75	79	806
Song Sparrow ( <i>Melospiza melodia</i> )	40	4	0.14	0.3	46	75	28
Golden-crowned Sparrow ( <i>Zonotrichia atricapilla</i> )	552	18	2.55	4.6	49	74	503
Dark-eyed Junco ( <i>Junco hyemalis</i> )	548	52	1.60	2.9	33	89	314
Common Redpoll ( <i>Carduelis flammea</i> )	444	44	2.18	3.9	82	88	394
<b>Residents</b>							
Downy Woodpecker ( <i>Picoides pubescens</i> )	7	45	0.03	0.1	na	—	—
Hairy Woodpecker ( <i>Picoides villosus</i> )	1	10	<0.01	<0.1	na	—	—
Steller's Jay ( <i>Cyanocitta stelleri</i> )	7	85	0.01	<0.1	na	—	—
Black-billed Magpie ( <i>Pica hudsonia</i> )	0	25	0.00	0.0	na	—	—
Common Raven ( <i>Corvus corax</i> )	0	86	0.00	0.0	na	—	—
Black-capped Chickadee ( <i>Poecile atricapillus</i> )	14	6	0.06	0.1	76	—	—
Chestnut-backed Chickadee ( <i>Poecile rufescens</i> )	218	81	0.85	1.5	56	90	162
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	366	75	1.25	2.2	37	91	245
Red Crossbill ( <i>Loxia curvirostra</i> )	4	30	0.01	<0.1	na	—	—
White-winged Crossbill ( <i>Loxia leucoptera</i> )	142	23	0.66	1.2	224	2	133
Pine Siskin ( <i>Carduelis pinus</i> )	275	37	1.28	2.2	199	47	144

<sup>a</sup> 1994–1999 captures or observations.

<sup>b</sup> 1995–1999 captures.

<sup>c</sup> Sample size based on all aged captures.

<sup>d</sup> Not calculated for captures  $\leq 30$ .

<sup>e</sup> Individuals only captured in 1994.

Nearctic-Nearctic migrant species (combined age classes:  $t = 2.28$ ,  $df = 16$ ,  $P = 0.037$ ). Ninety percent of the Alder Flycatchers, Wilson's Warblers, and Lincoln's Sparrows had passed through Yakutat by 7 September. Except for Lincoln's Sparrow, median passage dates for all other sparrows were later than they were for wood-warblers (Table 3). Male

Slate-colored Juncos (*Junco. h. hyemalis*) migrated significantly later than male Oregon Juncos (*J. h. oregonus*; only males could be readily identified to subspecies;  $\chi^2 = 8.31$ ,  $df = 1$ ,  $P = 0.004$ ). Except for Winter Wrens, 90% of all individuals of all other Nearctic-Neotropical and Nearctic-Nearctic species had passed through Yakutat by 1 October.

TABLE 3. Passage dates of post-breeding, small landbirds at Yakutat, Alaska, 1995–1999. Only taxa with >30 known-age (hatching-year and after-hatching-year combined) individuals are included. For test between age-class medians,  $df = 1$ . Species are arranged by migration-distance category.

Species	All ages		After-hatching-year		Hatching-year		$\chi^2$	P-value
	Median date	90% date range <sup>a</sup>	Median	n	Median	n		
<b>Nearctic-Neotropical migrants</b>								
Alder Flycatcher	16 Aug	4 Aug–4 Sep	9 Aug	10	19 Aug	32	9.18	0.003
Ruby-crowned Kinglet	20 Aug	2 Aug–22 Sep	26 Aug	136	19 Aug	687	11.99	0.001
Hermit Thrush	13 Sep	8 Aug–29 Sep	21 Sep	258	7 Sep	1,421	57.72	<0.001
Orange-crowned Warbler	24 Aug	3 Aug–21 Sep	31 Aug	706	20 Aug	1,109	128.39	<0.001
Yellow Warbler	2 Sep	16 Aug–21 Sep	5 Sep	223	31 Aug	428	40.95	<0.001
Yellow-rumped Warbler	23 Aug	4 Aug–23 Sep	28 Aug	56	21 Aug	332	11.37	0.001
Wilson's Warbler	12 Aug	2 Aug–1 Sep	17 Aug	101	10 Aug	348	17.76	<0.001
Savannah Sparrow	4 Sep	18 Aug–25 Sep	9 Sep	147	3 Sep	301	4.35	0.037
Lincoln's Sparrow	16 Aug	3 Aug–7 Sep	17 Aug	163	15 Aug	1,290	0.58	0.45
White-crowned Sparrow	3 Sep	21 Aug–24 Sep	5 Sep	3	2 Sep	72	0.61	0.43
<b>Nearctic-Nearctic migrants</b>								
Red-breasted Nuthatch	17 Aug	7 Aug–8 Sep	27 Aug	18	17 Aug	47	1.14	0.28
Winter Wren	14 Sep	17 Aug–4 Oct	14 Sep	6	14 Sep	56	0.15	0.70
Varied Thrush	4 Sep	3 Aug–27 Sep	14 Sep	16	4 Sep	65	0.05	0.82
Fox Sparrow	3 Sep	18 Aug–26 Sep	11 Sep	171	3 Sep	635	6.64	0.010
Song Sparrow	28 Aug	14 Aug–20 Sep	28 Aug	7	28 Aug	21	0.00	1.00
Golden-crowned Sparrow	15 Sep	29 Aug–26 Sep	16 Sep	133	15 Sep	370	14.61	<0.001
Slate-colored Junco <sup>b</sup>	18 Sep	26 Aug–1 Oct	20 Sep	2	18 Sep	23	0.37	0.54
Oregon Junco <sup>b</sup>	9 Sep	18 Aug–26 Sep	9 Sep	16	9 Sep	96	0.08	0.77
Common Redpoll	1 Sep	23 Aug–26 Sep	31 Aug	48	1 Sep	346	0.25	0.62
<b>Residents</b>								
Chestnut-backed Chickadee	6 Sep	5 Aug–1 Oct	7 Sep	17	6 Sep	145	0.00	1.00
Golden-crowned Kinglet	2 Sep	2 Aug–30 Sep	25 Aug	23	2 Sep	222	0.17	0.68
White-winged Crossbill	26 Sep	5 Sep–2 Oct	26 Sep	131	2 Oct	2	0.54	0.46
Pine Siskin	4 Sep	9 Aug–30 Sep	5 Sep	76	4 Sep	68	5.35	0.021

<sup>a</sup> Range of dates when  $\geq 90\%$  of all individuals passed through Yakutat.

<sup>b</sup> Only includes males.

TABLE 4. Mass of after-hatching-year (AHY) and hatching-year (HY) birds captured during post-breeding migration at Yakutat, Alaska, 1994–1999. Only species that had  $\geq 10$  known-age individuals within each age class are included. Species arranged by migration-distance category.

Species	Mean (g) $\pm$ SE (n)		t-value	P-value	HY:AHY mass
	AHY	HY			
<b>Nearctic-Neotropical migrants</b>					
Ruby-crowned Kinglet	6.63 $\pm$ 0.04 (114)	6.38 $\pm$ 0.02 (540)	6.460	<0.001	0.962
Hermit Thrush	24.84 $\pm$ 0.13 (197)	24.45 $\pm$ 0.05 (1,225)	2.786	0.006	0.984
Orange-crowned Warbler	9.51 $\pm$ 0.03 (484)	9.40 $\pm$ 0.03 (636)	2.595	0.010	0.998
Yellow Warbler	10.33 $\pm$ 0.06 (178)	9.90 $\pm$ 0.05 (291)	5.285	<0.001	0.958
Yellow-rumped Warbler	13.11 $\pm$ 0.14 (58)	12.78 $\pm$ 0.06 (225)	2.152	0.035	0.975
Wilson's Warbler	7.61 $\pm$ 0.05 (103)	7.48 $\pm$ 0.03 (245)	2.177	0.031	0.983
Savannah Sparrow	19.65 $\pm$ 0.24 (102)	18.97 $\pm$ 0.17 (206)	2.268	0.024	0.965
Lincoln's Sparrow	16.21 $\pm$ 0.12 (160)	15.77 $\pm$ 0.04 (999)	3.414	0.001	0.973
<b>Nearctic-Nearctic migrants</b>					
Red-breasted Nuthatch	10.96 $\pm$ 0.11 (17)	10.97 $\pm$ 0.14 (34)	-0.049	0.96	1.001
Varied Thrush	83.52 $\pm$ 1.76 (13)	82.75 $\pm$ 0.61 (59)	0.418	0.68	0.991
Fox Sparrow	36.98 $\pm$ 0.36 (75)	36.44 $\pm$ 0.18 (347)	1.343	0.18	0.985
Golden-crowned Sparrow	31.20 $\pm$ 0.57 (32)	31.15 $\pm$ 0.25 (213)	0.075	0.94	0.998
Common Redpoll	12.11 $\pm$ 0.34 (10)	12.16 $\pm$ 0.09 (89)	-0.151	0.88	1.004
<b>Residents</b>					
Chestnut-backed Chickadee	9.99 $\pm$ 0.16 (15)	10.14 $\pm$ 0.07 (88)	-0.840	0.41	1.015
Golden-crowned Kinglet	6.07 $\pm$ 0.08 (31)	6.29 $\pm$ 0.03 (126)	-2.496	0.017	1.036
Pine Siskin	13.04 $\pm$ 0.12 (45)	12.80 $\pm$ 0.18 (26)	1.081	0.29	0.982

In 70% of Nearctic-Neotropical migrant species, HY birds migrated significantly ( $P < 0.05$ ) earlier than adults (Table 3). Age did not influence migration timing among Lincoln's or White-crowned sparrows, but HY Alder Flycatchers migrated significantly later than adults (Table 3). Among Nearctic-Nearctic migrants, adult Fox ( $P = 0.010$ ) and Golden-crowned ( $P < 0.001$ ) sparrows migrated later than HY individuals. Timing was similar among age classes for the remaining species (Table 3).

Masses of HY birds were lower (all  $P \leq 0.035$ ) than those of AHY birds in all Nearctic-Neotropical migrants (Table 4). The proportional mass of HY individuals, relative to AHY individuals, decreased with increasing migration distance (i.e., migration category, Table 4; weighted least squares:  $F_{2,13} = 8.71$ ,  $P = 0.004$ ,  $R^2 = 0.57$ ). HY individuals of species that migrate to the Neotropics weighed proportionally less than Nearctic migrants, which weighed proportionally less than residents.

## DISCUSSION

Mist-net capture rates at our Yakutat banding station were among the highest recorded

at post-breeding banding stations in Alaska (see reports at [www.absc.usgs.gov/research/bpif/meetings.html](http://www.absc.usgs.gov/research/bpif/meetings.html)), and Nearctic-Neotropical migrants constituted a majority of the captures. Corresponding to the conclusions of Wang and Finch (2002), our mist-net samples were most effective for small landbirds but under-represented larger species (those  $> 50$  g). Relatively high capture rates at Yakutat, coupled with the small area we sampled (7.5 ha), support Isleib and Kessel's (1973) assertion that a substantial number of small landbirds undertake a post-breeding migration along the eastern Gulf of Alaska coastline. Additional support is provided by the relatively low inter-annual variation in capture rates of many common species, particularly of Nearctic-Neotropical migrants. Our casual observations suggest that post-breeding landbird migration is widespread across the Foreland's continuous mosaic of shrublands and shrubby meadows.

Species composition of post-breeding birds captured in mist nets and observed during mist netting was very similar to the breeding avifauna of Yakutat (Shortt 1939, Patten 1982, Andres and Browne 2005) and other coastal

regions of south-central Alaska (Gabrielson and Lincoln 1959, Isleib and Kessel 1973). Additionally, only coastal forms of Hermit Thrush, Orange-crowned Warbler, and Fox Sparrow were captured at Yakutat. The Gulf of Alaska coastline does not appear to be a major migration route for several common western Alaska species (Alder Flycatcher, Gray-cheeked Thrush, Blackpoll Warbler, and Northern Waterthrush). These species were much more abundant at Fairbanks than at Yakutat during post-breeding migration (Benson and Winker 2001). Alder Flycatchers, however, may have initiated migration prior to our netting effort. The Foreland periodically provides breeding, stopover, and winter habitat for irruptive species. Annual synchrony in capture rates of White-winged Crossbills, Common Redpolls, and Pine Siskins at Yakutat matched synchronous irruption patterns documented in western North America (Koenig 2001).

Off-site recoveries and recaptures, albeit few, suggest that migrants likely continue southward along the Pacific coast of North America. Although waterbirds are known to migrate in spring across the Gulf of Alaska (Myres 1972), the extent to which small landbirds make the same crossing remains unknown; however, the recovery of an HY Yellow Warbler on a fishing boat 17 km off the Yakutat area coastline provides some evidence that small landbirds might be undertaking at least short-distance, over-water crossings. The banding site of that Yellow Warbler was actually to the southwest of Yakutat, suggesting that some migrants may originate from areas to the west and southwest of Yakutat. Large numbers of Wilson's Warblers banded on the Alaska Peninsula did not appear at Yakutat (see reports at [www.absc.usgs.gov/research/bpif/meetings.html](http://www.absc.usgs.gov/research/bpif/meetings.html)). Additionally, many post-breeding passerine migrants have been encountered 80 km offshore on Middleton Island (59° 43' N, 146° 30' W; see fall reports in the serial, *North American Birds*).

In general, age ratios of migrant passerines vary markedly among sites and species (Ralph 1981, Woodrey and Chandler 1997, Woodrey 2000). Our study is one of the first to show consistently greater percentages of young sparrows relative to that of wood-warblers. Greater percentages of HY birds have been

captured at Pacific and Atlantic coast sites relative to corresponding inland sites (Murray 1966, Stewart et al. 1974, Mewaldt and Kaiser 1988, Morris et al. 1996, Humple and Geupel 2002). Ralph (1981) suggested that the high proportions of young birds on the coast delineated the periphery of a species' migratory pathway. That HY individuals were predominant (>90%) among captures of the rarest, and hence the most peripheral, species at our coastal Yakutat site supports Ralph's (1981) explanation. For the more common Yakutat species, age ratios are more comparable with those found at inland sites, suggesting that the eastern Gulf of Alaska coastline is a major route for many of the migrant species that we captured. Woodrey and Moore (1997) thought that more balanced age ratios observed along the northern Gulf of Mexico coast were a result of the flight barrier imposed by the open waters of the gulf. Tall mountains along the Gulf of Alaska coastline may impede a general eastward, inland flow of migrants. However, large birds, such as Sandhill Cranes (*Grus canadensis*), are known to use coastal river valleys to access interior migration pathways (Isleib and Kessel 1973, Patten 1982). The magnitude of small landbird migration through these river corridors, however, is unknown.

The greatest number of small landbird migrants pass through Yakutat between mid-August and mid-September. West of Yakutat at Cold Bay, migration also peaked in late August (Bailey 1974). Our daily mist-netting efforts ensured that we did not miss weather-related passages of large numbers of migrants in any given year. Weather, however, assuredly has some influence on the annual variability in capture rates (see DeSante 1983). At Cold Bay, migrants increased with the passage of fronts (Bailey 1974), a pattern we observed casually at Yakutat.

Rotenberry and Chandler (1999) suggested that southerly breeding wood-warblers initiated migration earlier than their counterparts to the north. At Yakutat, male Slate-colored Juncos, which do not breed at Yakutat, arrived much later than Oregon Junco males, which do breed there. Otherwise, the geographic similarity of the breeding avifauna of south-central Alaska and our inability to determine exact breeding origins of post-breeding mi-

grants captured at Yakutat mask any timing patterns influenced by geographic origins of post-breeding migrants.

The earlier passage of Yakutat's Nearctic-Neotropical migrants corresponds with the shorter breeding-range occupancy of high-latitude passerine migrants captured at Fairbanks, Alaska (Benson and Winker 2001). However, some species differed markedly in their migration timing between these two sites; HY Alder Flycatchers, Yellow Warblers, Savannah Sparrows, and White-crowned Sparrows passed through 10–16 days earlier at Fairbanks than they did at Yakutat, whereas HY Ruby-crowned Kinglets and Wilson's Warblers passed through 10–14 days later in Fairbanks. Some Alder Flycatchers and Wilson's Warblers may have passed through Yakutat before netting was initiated on 1 August. Hatching-year Orange-crowned Warblers, Yellow-rumped Warblers, Fox Sparrows, and Lincoln's Sparrows were similar in their migration timing at the two sites; timing patterns of AHY birds were similar to those of HY individuals at both sites.

Differences in age-related patterns of passerine migration generally arise from differences in timing and location (Woodrey 2000). The high percentage (70%) of Nearctic-Neotropical species among which HY birds preceded AHY individuals in migration corresponded to the age-related migration patterns observed at Fairbanks; there, in 64% of Nearctic-Neotropical species, HY birds preceded AHY birds (Benson and Winker 2001). There was complete consistency in the age-related passage of 10 migrant species shared between Yakutat and Fairbanks. Because we operated mist nets on a daily schedule, as did the Fairbanks station, age-related differences in migration timing were not due to temporal differences in sampling effort (Kelly and Finch 2000). Few other sites south of Alaska have shown such consistent age-related patterns in migration timing of short- and long-distance migrants. Mixing of geographically distinct populations at more southern sites may blur age-dependent migration patterns.

Hatching-year individuals may initiate southward movements sooner than adults because they are less efficient in procuring food resources needed to complete migration. Inefficiency is due to inexperience, social and

physiological constraints, or some combination of these factors (reviewed by Woodrey 2000). Alternatively, adult birds may delay migration until the completion of prebasic molt (reviewed by Gauthreaux 1982). That masses of many HY Yakutat migrants were less than those of AHY birds suggests that young birds are less efficient at performing their first migration. Mass differences between HY and AHY individuals are generally greatest in long-distance migrants at Yakutat, and at other migration sites (reviewed in Woodrey 2000); masses of resident HY and AHY birds at Yakutat were more equitable. Lower mass, and assumed low fat loads, would cause HY individuals to make shorter flights and hence prolong migration time. Accordingly, age-related differences in migration timing should dissipate as migrants approach their wintering areas and should be greatest nearer their breeding areas.

Clearly, the eastern Gulf of Alaska coastline provides an important pathway for small landbirds undertaking their post-breeding migration southward from Alaska. Because landbird stopover habitats are a fairly continuous element in the landscape matrix of south-central Alaska, we suspect that migratory populations are probably not limited by the amount or configuration of stopover habitat. Maintenance of high quality stopover habitats along the entire migration pathway, however, is needed to ensure successful migration of small landbirds, particularly for those completing their first southward migration.

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APPENDIX. Post-breeding migrants rarely captured or observed at Yakutat, Alaska, 1994–1999. Species arranged by migration-distance category.

Species	Number captured	% days observed
<b>Nearctic-Neotropical migrants</b>		
Rufous Hummingbird ( <i>Selasphorus rufus</i> )	8	1
Olive-sided Flycatcher ( <i>Contopus cooperi</i> )	0	1
Yellow-bellied Flycatcher ( <i>Empidonax flaviventris</i> )	1	0
Warbling Vireo ( <i>Vireo gilvus</i> )	6	1
Bank Swallow ( <i>Riparia riparia</i> )	0	1
Barn Swallow ( <i>Hirundo rustica</i> )	0	4
Gray-cheeked Thrush ( <i>Catharus minimus</i> )	1	<1
Swainson's Thrush ( <i>Catharus ustulatus</i> )	2	<1
American Pipit ( <i>Anthus rubescens</i> )	0	4
Tennessee Warbler ( <i>Vermivora peregrina</i> )	1	0
Blackpoll Warbler ( <i>Dendroica striata</i> )	2	<1
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	7	<1
Common Yellowthroat ( <i>Geothlypis trichas</i> )	7	1
Chipping Sparrow ( <i>Spizella passerina</i> )	1	0
Brewer's Sparrow ( <i>Spizella breweri</i> )	2	0
<b>Nearctic-Nearctic migrants</b>		
Red-breasted Sapsucker ( <i>Sphyrapicus ruber</i> )	0	2
Northern Shrike ( <i>Lanius excubitor</i> )	0	1
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	1	0
Lapland Longspur ( <i>Calcarius lapponicus</i> )	2	4
Rusty Blackbird ( <i>Euphagus carolinus</i> )	1	9
Brown-headed Cowbird ( <i>Molothrus ater</i> )	0	<1
<b>Residents</b>		
Northwestern Crow ( <i>Corvus caurinus</i> )	0	1
Pine Grosbeak ( <i>Pinicola enucleator</i> )	2	0

## VARIATION IN INCUBATION PATTERNS OF RED-WINGED BLACKBIRDS NESTING AT LAGOONS AND PONDS IN EASTERN ONTARIO

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**ABSTRACT.**—We studied incubation patterns and hatchability of Red-winged Blackbirds (*Agelaius phoeniceus*) nesting in two different wetland habitats—beaver ponds and sewage lagoons—in eastern Ontario during 1999–2001. We presumed that, if incubating Red-winged Blackbirds could acquire food more readily at sewage lagoons than at beaver ponds, they should respond by taking fewer and shorter foraging bouts, which would result in longer bouts of attentiveness, shorter incubation periods, and higher hatchability of eggs. Although differences were small, female foraging bouts were shorter and bouts of attentiveness were longer at sewage lagoons than they were at beaver ponds. Incubation constancies were subsequently greater, and, ultimately, incubation periods at sewage lagoons were shorter. Shorter incubation periods at sewage lagoons, however, did not result in increased hatchability. Our results suggest that, in habitats where incubating Red-winged Blackbirds can acquire food more readily, incubation periods may become shorter and incubation constancies may become higher. Received 7 September 2004, accepted 28 April 2005.

Many species of temperate-zone passerines modify incubation patterns in response to variation in nutrient availability (Hebert 2002, Eikenaar et al. 2003), frequency of mate feeding (Nilsson and Smith 1988, Pearse et al. 2004, Radford 2004), body mass (Williams 1991), temperature (Conway and Martin 2000a, Reid et al. 2002), and nest predation (Martin and Ghalambor 1999, Conway and Martin 2000b, Ghalambor and Martin 2002). Eggs of most passerines must be maintained at a temperature of 34–39° C for optimal embryonic development (Drent 1975, Webb 1987, Williams 1996). Ambient temperatures, however, rarely remain within this range, and deviations in egg temperatures can affect incubation period and egg hatchability (Strausberger 1998); therefore, incubation by parents is required to prevent embryos from chilling or overheating.

When ambient temperatures are low, incubation can be energetically demanding for parents, requiring an increase in metabolic rate to a level approaching that experienced during chick-rearing (Williams 1996, Thomson et al. 1998, Visser and Lessells 2001). Hence, energetic demands during incubation may have fitness consequences: adult body condition may deteriorate, or adults may be

unable to provide conditions conducive to embryonic development. Fitness consequences will be especially severe where only the female incubates (gyneparental systems) and where bouts of attentiveness are interspersed with foraging bouts (Williams 1996).

In gyneparental systems, daytime incubation is usually intermittent because females must balance the time spent foraging against the thermal needs of the developing embryos and the energetic demands of rewarming the clutch after a foraging bout. Most reviews of avian incubation suggest that the duration of attentiveness bouts (interval during which the female incubates between two foraging bouts) is dictated by the female's energy needs (Kendeigh 1952, Haftorn 1978, Weathers and Sullivan 1989, but see Conway and Martin 2000b). If the energy needs of the female are an important factor affecting incubation patterns, then nest attentiveness should increase in relation to the rate at which food can be acquired (i.e., food acquisition) during foraging bouts, the incubation period should be shorter, and hatching success should increase (Martin 1987). Thus, species that use more energetically expensive foraging strategies or forage in habitats where food items are less available may have to spend more time foraging or engage in more frequent foraging bouts to meet nutritional requirements.

Although there have been few studies of variation in passerine incubation patterns, presumably because these data are time-consum-

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ing and laborious to collect, results from several of these studies (e.g., Nilsson and Smith 1988, Moreno 1989, Sanz 1996, Pearse et al. 2004) suggest an important relationship between nutrient availability and incubation patterns. For example, studies on Northern Wheatears (*Oenanthe oenanthe*; Moreno 1989), Blue Tits (*Parus caeruleus*; Nilsson and Smith 1988), and Pied Flycatchers (*Ficedula hypoleuca*; Sanz 1996) have revealed that females receiving supplemental food during incubation had significantly shorter incubation periods and/or their clutches experienced greater hatchability (but see Pearse et al. 2004). Moreover, there should be a premium on short incubation periods, which reduce the time that eggs are vulnerable to predators (Clark and Wilson 1981, Conway and Martin 2000a, Martin 2002).

As far as we know, there have been no studies that have evaluated variation in incubation patterns related to foraging habits or food acquisition between habitats. Using a comparative approach, Reid et al. (1999) suggested that the duration of foraging bouts among European Starlings (*Sturnus vulgaris*) was more than four times longer (20 min versus 4.5 min) on Waddensea Island (from Drent et al. 1985) than on Fair Isle, where incubating adults could feed in close proximity to their nest cavities, reducing the time and energy needed to travel to foraging areas. In addition, Reid et al. (1999) suggested that, because the ground on Fair Isle remained permanently damp, it was unlikely that the starling's invertebrate prey would be difficult to obtain during any period of the day. However, because Waddensea Island and Fair Isle differ substantially in latitude, climate, and habitat, comparison of incubation patterns between these islands was not feasible (Reid et al. 1999).

We examined habitat-related variation on gyneparental incubation patterns, incubation periods, and hatchability of eggs by studying Red-winged Blackbirds (*Agelaius phoeniceus*) nesting at numerous sewage lagoons and beaver ponds in eastern Ontario. Extensive data have suggested that food availability is greater at sewage lagoons than in other habitats during the breeding season of many bird species (e.g., Swanson 1977, Piest and Sowls 1985, Hussell and Quinney 1987, Porter 1993, Zimmerling 2002). For example, during laying, in-

cluding a natural cattail marsh (Hussell and Quinney 1987). During the brood-rearing period in eastern Ontario, female Red-winged Blackbirds at sewage lagoons captured a mean of nine insects per foraging bout, whereas females at beaver ponds captured one to two insects per foraging bout (Zimmerling 2002). Therefore, we predicted that females nesting at sewage lagoons would take fewer and shorter foraging bouts than females nesting at beaver ponds. Consequently, we also predicted that incubation periods would be shorter and egg hatchability greater at sewage lagoons.

## METHODS

*Study area.*—From 1999 to 2001, we studied Red-winged Blackbirds nesting at wetlands in eastern Ontario between Cobden (45° 40' N, 77° 10' W) and Vankleek Hill (45° 35' N, 74° 40' W; see Zimmerling 2002). Wetlands in the study area included 19 small (0.3–3 ha) beaver ponds (hereafter, ponds) and 10 municipal sewage lagoon complexes (secondary wastewater treatment facilities; hereafter, lagoons). On average, lagoon complexes were composed of three individual lagoons or "cells" (range = 1–7), but not all cells supported nesting Red-winged Blackbirds. We sampled 10, 14, and 19 ponds in 1999, 2000, and 2001, respectively. Cattails (*Typha* spp.) dominated the emergent vegetation at both ponds and lagoons, but, relative to ponds, lagoons had only a thin strip of cattails around their perimeters. Most lagoon complexes were bordered by agricultural crops and old-fields, but mixed deciduous forests partially bordered several lagoons. Ponds were bordered mainly by old-fields and mixed deciduous forests.

Time of ice breakup during early spring was similar on lagoons and ponds, with the exception of one aerated lagoon cell that became ice-free earlier. During the study period, water levels in ponds did not fluctuate >1 m, either seasonally or annually. In contrast, average water depth within and among sewage lagoon complexes varied seasonally between 2 and 5 m, but large fluctuations in water depth usually occurred outside of the Red-

winged Blackbird's breeding season. In 2000, water levels at 7 of 10 lagoon sites were lowered in mid-May; thus, only the remaining three lagoons were sampled.

Despite obvious physical differences between lagoons and ponds, Zimmerling (2002) showed that populations of female Red-winged Blackbirds in the eastern Ontario study area were demographically (juvenile: adult) similar and that morphological characteristics (i.e., culmen, wing chord, tarsus length, and body mass) of females also did not differ between habitats. In addition, although lagoons and ponds differed marginally in shape and size, the maximum number of active nests/1,000 m<sup>2</sup> of wetland (based on measurements of wetland perimeters) were similar between habitats (Zimmerling 2002). In contrast, the maximum number of active nests/1,000 m<sup>2</sup> of emergent vegetation (*Typha* spp.) within wetlands was four times higher at lagoons than at ponds (8.4 versus 2.1) because suitable nesting habitat (i.e., emergent vegetation) was restricted.

**Field methods.**—Nests were discovered during twice-weekly searches of emergent vegetation. Nests were marked with flagging tape and monitored daily. Using remote temperature sensors (Hobo Temp XT, Onset Computer Co., Pocasset, Massachusetts), we assessed incubation patterns of female Red-winged Blackbirds at 406 nests (1999, 2000, and 2001,  $n = 59/45$  [lagoon/pond], 38/69, and 115/80, respectively). After the second egg of a clutch was laid, but before the third egg was laid, a thermistor attached to a Hobo Temp data logger was slowly worked into the nest from underneath until it was <5 mm above the nest lining. The thermistor was set <5 mm above the nest lining to prevent contact with the incubating female's brood patch. Thermistors set higher than this level were usually discovered and physically removed by the female, and, on six occasions, the nest was abandoned. To minimize detection by incubating females and predators, data loggers were wrapped in plastic and concealed in vegetation 2 to 6 m from the nest.

Data loggers continuously recorded temperature variations at 2.5-min intervals for up to 13 consecutive days, which spanned the entire incubation period (a 2.5-min sampling interval was the shortest possible interval that

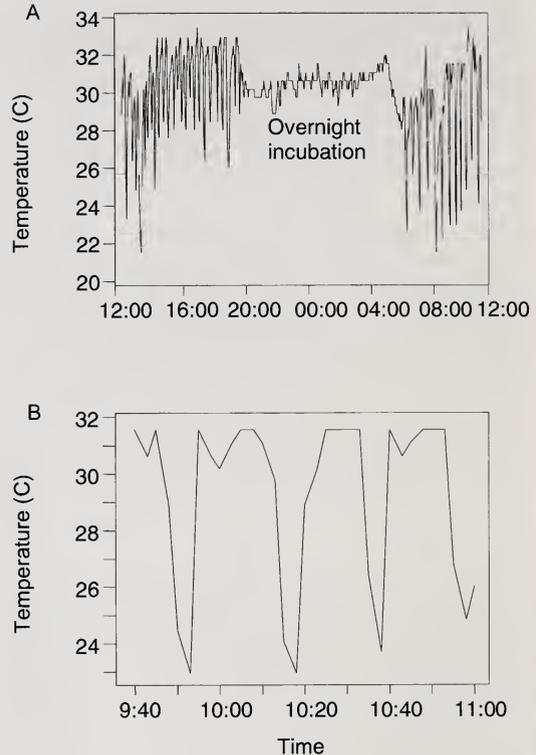


FIG. 1. (A) Temperature recorded at a single Red-winged Blackbird nest at a lagoon in Perth, Ontario over a 24-hr period, 2–3 June 2001. The overnight incubation session lasted from 19:53 to 06:53 EST. (B) An expanded 90-min section of this trace shows high nest temperature when the parent is incubating and sharply falling temperature during daytime foraging bouts when the nest is left unattended. Arrivals and departures of the incubating adult result in sudden, obvious changes in nest temperature.

could be maintained for 13 days without overloading the logger's memory capacity). After hatching was complete (i.e., when 2 days had elapsed since the last egg hatched), data loggers and thermistors were removed from nests.

Incubation patterns were extracted after downloading data from loggers using Boxcar Pro 4.0 software (Onset Computer Co., Pocasset, Massachusetts). Because thermistors did not contact the female's brood patch, but instead, recorded air temperature at the bottom of the nest bowl, recorded temperatures were lower than the 34–39°C temperatures required for optimal embryo development (Fig. 1). Nonetheless, periods when a female was incubating versus absent from the nest showed

as clear peaks and troughs on the temperature traces, allowing times of arrival and departure to be estimated. We acknowledge that data regarding time periods are estimates due to factors such as lags in temperature changes and data loggers recording temperature every 2.5 min rather than continuously; however, combining a large number of readings ( $n = 6,300\text{--}7,400$ ) over the course of the incubation period, and considering that these factors should have affected birds similarly in pond and lagoon habitats, their effects should have been minimal. To verify that arrival and departure times were accurately discerned from temperature traces, we positioned video cameras (Sony 8 mm Handycams) 10 m from a subset of nests ( $n = 6$ ) and video-recorded female incubation patterns for 1 hr (6 hr total). Comparisons of video recordings and temperature traces ( $n = 144$  data points) indicated that departure and arrival times at the nest were accurately identified from the temperature traces. On the basis of these observations, we interpreted any drop in temperature of more than  $4^{\circ}\text{C}$  that occurred within a 5-min period as a departure from the nest (i.e., the start of a foraging bout). Any similar rise in temperature signified an arrival at the nest (initiating a bout of attentiveness). Hence, during the daytime (06:00–20:00 EST), duration of foraging bout was calculated as the number of minutes between two successive bouts of attentiveness. Duration of attentiveness bout was calculated as the number of minutes between two successive foraging bouts. Because duration of attentiveness and foraging bouts may be influenced by number of foraging bouts, we calculated the number of foraging bouts/hr as the number of foraging bouts/total hr of daylight. We also calculated incubation constancy (percentage of daytime spent incubating) as total duration of attentiveness bout / (total duration of attentiveness bout + total duration of foraging bout) to evaluate whether differences, if any, in duration of attentiveness or foraging bouts and/or number of foraging bouts/hr influenced incubation constancy. Because variation in the duration of overnight incubation could indicate differential use of endogenous reserves, we calculated overnight incubation as the number of minutes between returning to the nest for the last time in the evening and leaving the nest the first time in

the morning. Females never left the nest during the night.

Temperature traces for nests with data loggers confirmed that onset of incubation in Red-winged Blackbirds occurs with the laying of the penultimate egg (e.g., Yasukawa and Searcy 1995). For nests without data loggers, incubation onset was assumed to have occurred once the penultimate egg was laid, but was also confirmed by temperature of the clutch. Nine days after incubation onset, nests with and without data loggers were checked daily to determine hatch date. Because Red-winged Blackbird clutches sometimes hatch asynchronously (Yasukawa and Searcy 1995), nests were visited at least once daily during hatching to record the sequence of hatching and to determine length of the incubation period (calculated as the time between laying of the penultimate egg and when the majority of eggs had hatched). However, in 1999, some nests were monitored only every other day, in which case nestling age ( $\pm 6$  hr) was estimated based on nestling size and wetness of their natal down (Zimmerling 2002). After hatching was complete, hatchability (i.e., number of eggs hatched/total number of eggs laid) was recorded.

Between 3 and 18 June 2001, we quantified foraging behavior for a subset of incubating females ( $n_{\text{lagoon}} = 7$  and  $n_{\text{pond}} = 5$ ) at two sewage lagoons (one bordered by agricultural fields and one partially bordered by uplands) and three beaver ponds. Most birds in the study area were not color-banded, but we identified individual females by following them away from their nests when observing them during foraging bouts. Foraging observations were conducted between 07:00 and 12:00 and began when the female left the nest and ended when the female returned to the nest (one data point per individual). For each female, we recorded the habitat(s) in which she foraged (i.e., emergent vegetation, shoreline, or forest-edge) and mean distance of foraging habitat(s) from the nest.

*Statistical analyses.*—We obtained relatively few temperature traces that covered the entire incubation period of a nest ( $n_{\text{lagoon}} = 19$ ,  $n_{\text{pond}} = 15$ ). For statistical analysis, we included all temperature traces with a minimum of 8 days of continuous recording during incubation ( $n_{\text{lagoon}} = 43$ ,  $n_{\text{pond}} = 39$ ) to increase

total sample size ( $n_{\text{lagoon}} = 62$ ,  $n_{\text{pond}} = 54$ ). Incomplete temperature traces were usually the result of nest predation or the female removing the thermistor during incubation; these were excluded from the analysis. We calculated mean incubation constancy (%), mean number of foraging bouts/hr, mean bout duration of attentiveness (min) and foraging (min), and mean overnight incubation (min) for all temperature traces with  $\geq 8$  days of continuous recording. For analysis of incubation period and hatchability, we combined datasets from nests with and without data loggers ( $n_{\text{lagoon}} = 138$ ,  $n_{\text{pond}} = 107$ ). To analyze hatchability, all eggs lost at active nests by causes other than hatching failure (i.e., predation, drowning, nest collapse, or clutch desertion) were excluded.

We used an information-theoretic approach for model selection (Burnham and Anderson 1998). We considered several *a priori* candidate models for each response variable that included main effects and a subset of interactions that were of interest. Model selection was done using Akaike's Information Criterion (AIC) with corrections for small sample size ( $AIC_c$ ) using PROC MIXED (SAS Institute, Inc. 2001) with the IC option for model estimation. Models were ranked using  $\Delta AIC_c$  (Burnham and Anderson 1998) and were calculated as  $\Delta AIC_c = AIC_{c_i} - AIC_{c_{\text{min}}}$  where  $\Delta AIC_{c_i}$  was the  $i^{\text{th}}$  model from a candidate set. Akaike weights ( $w_i$ ) were calculated to assess the relative likelihood of each model being the best model.

Because we were interested in the effects of habitat-related differences in incubation patterns of female Red-winged Blackbirds, all candidate models included effects of habitat (lagoon versus pond) as an explanatory variable. Because incubation patterns in some species may vary temporally (e.g., Conway and Martin 2000b), year (coded 1, 2, 3 for 1999, 2000, and 2001, respectively) and nest-initiation date (date first egg was laid; May 1 = 1) were also used to generate a set of candidate models. Model selection was done separately for incubation period, incubation constancy, duration of foraging bout, foraging bouts/hr, duration of attentiveness bout, duration of overnight incubation, and hatchability, respectively. The set of candidate models was the same for each dependent variable and includ-

ed effect of habitat (HAB), nest-initiation date (ID), year (YR), and all two-way interactions involving habitat. A null model (intercept only) was also included as a candidate model. Only candidate models with  $\Delta AIC_c < 2.0$  are presented. When no candidate models had  $\Delta AIC_c < 2.0$ , second-best models are presented.

## RESULTS

*Incubation period.*—The best model explained 14% of variation in incubation period and included habitat (HAB), year (YR), and habitat-by-year interaction ( $HAB \times YR$ ) as predictors (Table 1). Likelihood of model fit for {HAB, YR,  $HAB \times YR$ } was  $>9\times$  that of the second-best model ({HAB, YR, ID,  $HAB \times YR$ },  $\Delta AIC_c = 4.4$ ). Incubation period was longer at ponds than at lagoons, but this difference varied with year. In 1999, incubation period was 0.8 days longer at ponds than at lagoons, but was only 0.2 days longer in each of the following 2 years.

*Incubation constancy.*—The model {HAB} was superior to other models considered, and explained 9% of variation in incubation constancy (Table 1). Likelihood of model fit for {HAB} was  $>5\times$  that of the second-best model ({HAB, YR,  $HAB \times YR$ },  $\Delta AIC_c = 3.5$ ). Incubation constancy was 4% lower at ponds than at lagoons (69% versus 73%) and this difference did not vary with nest-initiation date or year.

*Duration of foraging bout.*—The best model explained 12% of variation in duration of foraging bout and included habitat (HAB), initiation date (ID), and habitat-by-initiation date ( $HAB \times ID$ ) interaction as predictors (Table 1). Likelihood of model fit for {HAB, ID,  $HAB \times ID$ } was  $>4\times$  that of the second-best model ({HAB, ID},  $\Delta AIC_c = 3.2$ ). Duration of foraging bout averaged longer at ponds (8.9 min) than at lagoons (8.1 min) and the difference increased with nest-initiation date.

*Foraging bouts/hr.*—We found considerable model-selection uncertainty for foraging bouts/hr and no predictors appeared particularly important (Table 1). Moreover, the null model, which contained no predictors, had the lowest  $AIC_c$  score of any models. Even the most complex model {HAB, ID, YR,  $HAB \times ID$ ,  $HAB \times YR$ } explained only 3% of variation in foraging bouts/hr.

TABLE 1. Model selection for variation in incubation period<sup>a</sup> (days), incubation constancy (%), duration of foraging bout (min), foraging bouts/hr, duration of attentiveness bout (min), duration of overnight incubation (min), and hatchability<sup>a,b</sup> of female Red-winged Blackbirds nesting at lagoons ( $n = 62$ ) and at ponds ( $n = 54$ ) in eastern Ontario, in relation to habitat (HAB, pond versus lagoon), nest-initiation date (ID, May 1 = 1), and year (YR, 1999–2001). Shown for each model are numbers of parameters (K), AIC difference with correction for small sample sizes ( $\Delta AIC_c$ ), model weight ( $w_i$ ), proportion of variance explained ( $R^2$ ), and Least Square Means  $\pm$  SE.

Response variable	Model	K	$\Delta AIC_c$	$w_i$	$R^2$	Ponds	Lagoons
Incubation period	HAB, YR, HAB $\times$ YR	7	0.0	0.896	0.14	12.4 $\pm$ 0.1	12.0 $\pm$ 0.1
	1999					12.7 $\pm$ 0.1	11.9 $\pm$ 0.1
	2000					12.6 $\pm$ 0.1	12.4 $\pm$ 0.1
	2001					12.1 $\pm$ 0.1	11.9 $\pm$ 0.1
	HAB, YR, ID, HAB $\times$ YR	8	4.4	0.099	0.15	12.4 $\pm$ 0.1	12.0 $\pm$ 0.1
Incubation constancy	HAB	3	0.0	0.851	0.09	69.3 $\pm$ 0.1	73.4 $\pm$ 0.1
	HAB, YR, HAB $\times$ YR	7	3.5	0.147	0.09	69.3 $\pm$ 0.1	73.1 $\pm$ 0.1
Duration of foraging bout	HAB, ID, HAB $\times$ ID	5	0.0	0.801	0.12	8.9 $\pm$ 0.2	8.1 $\pm$ 0.2
	HAB, ID	4	3.2	0.171	0.06	8.6 $\pm$ 0.2	8.0 $\pm$ 0.2
Foraging bouts/hr	NULL	2	0.0	0.689	0.00		
	HAB	3	1.8	0.280	0.01	2.2 $\pm$ 0.1	2.1 $\pm$ 0.1
Duration of attentiveness bout	HAB, ID	4	0.0	0.638	0.06	30.6 $\pm$ 1.6	32.2 $\pm$ 1.5
	HAB, ID, HAB $\times$ ID	5	1.4	0.316	0.06	30.6 $\pm$ 1.5	32.1 $\pm$ 1.5
Duration of overnight incubation	NULL	2	0.0	0.883	0.00		
	HAB	3	3.2	0.059	0.01	537.5 $\pm$ 11.5	545.1 $\pm$ 12.8
	HAB	3	4.8	0.083	0.01	87.8 $\pm$ 0.1	85.6 $\pm$ 0.1

<sup>a</sup> Number of nests in model = 361 (161 pond, 200 lagoon).

<sup>b</sup> Total number of eggs = 1,353 (581 pond, 772 lagoon).

*Duration of attentiveness bout.*—The model {HAB, ID} was superior to other models considered and explained 6% of variation in duration of attentiveness bout (Table 1). Likelihood of model fit for {HAB, ID} was 2 $\times$  that of the second-best model ({HAB, ID, HAB  $\times$  ID},  $\Delta AIC_c = 1.4$ ), which also contained nest-initiation date as a predictor. Duration of attentiveness bout was 1.6 min shorter at ponds than at lagoons. Regardless of habitat, the duration of attentiveness bout increased by 0.3 min for each later day of nest initiation.

*Duration of overnight incubation.*—There was considerable model-selection uncertainty for duration of overnight incubation and no predictors appeared particularly important (Table 1). Moreover, the null model, which contained no predictors, had the lowest  $AIC_c$  score of any models considered. Even the most complex model {HAB, ID, YR, HAB  $\times$  ID, HAB  $\times$  YR} explained only 2% of variation in duration of overnight incubation.

*Hatchability.*—Model selection for variation in egg hatchability was equivocal and no predictors in the set of candidate models appeared important (Table 1). Moreover, the null model, which contained no predictors, had the lowest  $AIC_c$  score of any models considered. Furthermore, among the set of candidate models, the most complex model {HAB, ID, YR, HAB  $\times$  ID, HAB  $\times$  YR} explained only 3% of the variation in hatchability.

*Foraging behavior.*—Incubating females nesting at ponds foraged >2 $\times$  farther away from their nests than did females nesting at lagoons (94  $\pm$  38 m versus 46  $\pm$  23 m). At ponds, all five females foraged within forest edges, although one female was observed capturing a flying insect (Odonata) over emergent vegetation. At lagoons, incubating females always foraged within the emergent vegetation, but on three occasions, they also foraged along lagoon shorelines.

## DISCUSSION

Many studies have demonstrated that insect abundance is greater (or insects are more easily acquired) at sewage lagoons than in other habitats (e.g., Swanson 1977, Piest and Sowls 1985, Porter 1993, Zimmerling 2002). Quinney (1983) showed that insect biomass at a sewage lagoon in southwestern Ontario was approximately 10 times greater than that at a nearby field habitat during the period when most Tree Swallows were incubating eggs. Many of these same studies also have revealed that the type of insects available to birds at sewage lagoons is different from that available in other habitats (e.g., Swanson 1977, Quinney 1983, Zimmerling 2002). During brood-rearing, Zimmerling (2002) found that female Red-winged Blackbirds at sewage lagoons in eastern Ontario usually foraged close to their nests and captured numerous flying insects (Family Chironomidae), whereas females at beaver ponds generally foraged much farther from their nests, often in adjacent uplands, and usually returned to the nest with one and sometimes two large insects, often from the Family Noctuidae (Zimmerling 2002). Thus, presuming that insect availability and/or the type of insects available at lagoons and ponds were different, we could examine the response of Red-winged Blackbird incubation patterns, incubation period, and hatchability of eggs to habitat-related differences in foraging behavior.

Incubation periods of Red-winged Blackbirds at lagoons were shorter than those at ponds. Other investigators (see references in Martin 1987, Williams 1996, Hebert 2002) have suggested that shorter incubation periods are a consequence of increased attentiveness during incubation. At lagoons, incubation constancy was 4% higher than it was at ponds, but because substantial variation in Red-winged Blackbird incubation constancy (range = 65–72%) has been reported elsewhere (e.g., Holcomb 1974), these results should be interpreted cautiously. Nonetheless, our results suggest that lower nest attentiveness at ponds compared with that at lagoons could be explained by habitat-related differences in foraging behavior, resulting in longer duration of foraging bouts and shorter duration of attentiveness bouts without changing the frequency

of foraging bouts. For example, although our behavioral observations were limited, female blackbirds incubating at ponds—unlike females at lagoons—did not forage within the emergent vegetation in close proximity to the nest; rather, they foraged much farther from the nest along forest-edges of woodlots bordering the ponds. Our behavioral observations of female foraging habits at ponds were similar to those found in other studies: marsh-nesting female Red-winged Blackbirds spend much of their time foraging in uplands that border their nesting habitat (e.g., Orians 1980, 1985; Whittingham and Robertson 1994; Turner and McCarty 1998) because of limited food availability within the marsh. It seems unlikely that food availability was limited within sewage lagoons in our study area because, even at the lagoon bordered by upland habitat, females were observed foraging only in the emergent vegetation and/or along the shoreline.

Although it was not possible to taxonomically categorize insects taken by foraging females during incubation, other studies in eastern Ontario have revealed that, during the brood-rearing period, females that foraged in upland habitats consistently delivered lepidopteran larvae to their broods (Bendell and Weatherhead 1982, Zimmerling 2002). Less than 65 km from our study area, Bendell and Weatherhead (1982) showed that female Red-winged Blackbirds fed lepidopteran larvae of the family Noctuidae (55% by volume) to their nestlings, of which larvae of a single species, *Amphipoea velata* (Walker), made up 31% of the total volume. In contrast, female passerines nesting at sewage lagoons feed nestlings chironomid adults (Quinney 1983, Zimmerling 2002), the most abundant insect at lagoons (Swanson 1977, Hussell and Quinney 1987). It is possible that female Red-winged Blackbirds incubating at ponds were searching for lepidopteran larvae in the upland habitats during foraging bouts, and, because many lepidopterans are cryptically colored, additional search time may have been required for females to find these insects. Therefore, female Red-winged Blackbirds foraging in upland habitats in eastern Ontario may have incurred costs associated with increased travel time and energy expenditure for food gathering, which may have resulted in longer for-

aging bouts, shorter bouts of attentiveness, and, ultimately, longer incubation periods.

We found annual variation in incubation patterns and incubation period, which may have been attributable to annual environmental variability. We are aware of only two studies of passerines that assessed annual variation in food supply and incubation patterns (Drent et al. 1985, Moreno 1989). Moreno (1989) found that, during the coldest year of his study, incubation length was negatively correlated with the amount of supplemented food he provided to incubating female Northern Wheatears. Similarly, Drent et al. (1985) found that when European Starlings' (*Sturnus vulgaris*) principle prey, crane fly larvae (*Tipula paludosa*), were scarce, incubating females responded by decreasing incubation constancy and increasing the length of foraging bouts. Relatively warm spring temperatures in 1999 in eastern Ontario may, in part, explain the nearly 1-day difference in incubation period between lagoons and ponds in 1999 compared with 2000 and 2001. Mean monthly temperature for May 1999 was 16.5° C, which was 3° and 2° C warmer than in 2000 and 2001, respectively. It is unlikely that annual variation in incubation period and differences observed between lagoons and ponds were the direct result of ambient temperature because both habitat types were sampled throughout eastern Ontario. Instead, differences in incubation period may have been due to habitat-related differences in type and/or abundance of insects available to incubating females. For example, the largest emergence of chironomids at two lagoon sites in eastern Ontario occurred 6 and 4 days earlier in 1999 than in 2000 and 2001, respectively (JRZ pers. obs.). Regardless, we did not assess dietary habits of incubating females (neither were they assessed in other studies of Red-winged Blackbirds); thus, we cannot preclude the possibility that other factors were responsible for annual variation in incubation period within and between habitats.

The importance of habitat and food availability in affecting seasonal variation in passerine incubation patterns is equivocal because nest attentiveness is positively correlated with ambient temperature in north-temperate environments (Zerba and Morton 1983, Conway and Martin 2000a). Conway and

Martin (2000a) proposed that the metabolic energy required by small birds during incubation decreases with increased ambient temperature and should allow individuals to increase length of attentiveness bouts because they are metabolizing energy reserves more slowly. In our study, duration of attentiveness bout increased with nest-initiation date, which was a proxy for increasing ambient temperatures during spring and summer. Food availability also may have increased (whether directly or indirectly) with ambient temperature during May, when the majority of females were incubating (also see Quinney 1983). Thus, increased rates of food acquisition (in response to increased food availability) may explain the decline in duration of foraging bout with nest-initiation date in both habitats. Not surprisingly, because of inherent difficulties in separating the effects of ambient temperature and food availability, few passerine studies, including ours, have unambiguously demonstrated a relationship between seasonal changes in incubation patterns and food availability.

It is possible that incubation patterns of female Red-winged Blackbirds did not differ between wetland habitats due to differential female foraging habits, but, rather, to differences in female age, female body size, nest predation, or the use of endogenous reserves. However, Red-winged Blackbird populations at lagoons and ponds in our study area were similar with respect to female age structure, body mass, and structural size (Zimmerling 2002). Moreover, Wheelwright and Beagley (2005) suggested that incubation behavior in Savannah Sparrows (*Passerculus sandwichensis*) is largely innate and unaffected by prior reproductive experience or other age-related variables. Other studies have suggested that predation risk can be an important factor influencing incubation behavior in some passerines (e.g., Ghalambor and Martin 2002, Martin 2002). However, in eastern Ontario, the proportion of Red-winged Blackbird nests depredated during incubation at beaver ponds, sewage lagoons, and roadside ditches (which resemble lagoons in vegetation structure) was similar, despite differences in primary predators (i.e., avian versus mammalian) in each habitat (JRZ unpubl. data). Although little is known about use of endogenous reserves by

incubating passerines, most studies indicate that passerines use exogenous nutrients for incubation (see Williams 1996, Conway and Martin 2000b). Some studies have shown mass loss by incubating females, but that may have been due to post-laying atrophy of reproductive organs rather than to loss of somatic tissue (Ricklefs and Hussell 1984). Moreover, overnight incubation represents a prolonged period of fasting coinciding with minimum daily ambient temperatures; therefore, if endogenous reserves were used more heavily by Red-winged Blackbirds at lagoons than at ponds, then duration of overnight incubation should have been longer at lagoons, but it was not. To better assess whether endogenous reserves were used differentially during incubation by female Red-winged Blackbirds nesting at lagoons, researchers should compare levels of endogenous reserves between onset and termination of overnight incubation.

In some species, shorter incubation periods and bouts of attentiveness can improve hatching success, which is influenced by temperature of eggs during incubation (Lyon and Montgomerie 1985, Nilsson and Smith 1988, Strausberger 1998; but see Eikenaar et al. 2003). We did not, however, detect a difference in hatchability of Red-winged Blackbird eggs between lagoons and ponds (85.6% versus 87.8%). Unlike some passerines that nest in the high arctic and take long foraging bouts (i.e., 20 min; Lyon and Montgomerie 1985, 1987), female Red-winged Blackbirds nesting at both lagoons and ponds generally took short foraging bouts (i.e., <10 min; also see Holcomb 1974), perhaps explaining the similarity in egg hatchability between habitat types. In other studies of Red-winged Blackbirds, egg hatchability ranged from 87.9% (Williams 1940) to 97.0% (Young 1963). It is possible that when egg size measurements were taken (for another study), some of the eggs in this study were damaged (dimpled or hairline cracked) by calipers, thus accounting for the relatively low hatchability of Red-winged Blackbird eggs in both habitats.

Comparisons of Red-winged Blackbirds nesting in two different habitats—sewage lagoons and beaver ponds—in eastern Ontario suggested that differences in incubation periods, incubation constancy, and bout duration

of attentiveness and foraging may have been responses to differential foraging habits, possibly as a result of differences in food acquisition during incubation. Differences in foraging habits, however, did not affect hatchability. Until further research and experimental work is extended to many other species, it will be difficult to judge the importance of variation in foraging habits and/or food acquisition in influencing incubation patterns and hatchability in passerines.

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## SEASONAL VARIATION IN ACTIVITY PATTERNS OF JUVENILE LILAC-CROWNED PARROTS IN TROPICAL DRY FOREST

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**ABSTRACT.**—We used radio-telemetry techniques to determine hourly activity patterns of 29 juvenile Lilac-crowned Parrots (*Amazona finschi*) during 1996–2000 in tropical dry forest of Jalisco, Mexico. Parrots had two peak activity periods—early morning and late afternoon—for both overall activity and local movement. Individuals were generally inactive and did not change location for 5–6 hr during the middle of the day. Parrots were more active in the dry season than in the rainy season, although movements resulting in a change of location did not vary between seasons. Seasonal variations in activity of Lilac-crowned Parrots may be related to variations in food availability or temperature. Activity patterns of parrots need to be considered when evaluating habitat use or survey data. Received 1 October 2004, accepted 26 April 2005.

When evaluating habitat use, the time of day and the activity being performed by an animal need to be considered, because animals select particular habitats for specific types of activity (Palomares and Delibes 1992). Often, however, studies of habitat use do not take into account activity or inactivity of the individual (Palomares and Delibes 1992).

Daily activity patterns of psittacines have been estimated indirectly from survey data on the frequency of flock encounters, with greater flock activity occurring in the early morning and late afternoon (Snyder et al. 1987, Gilardi and Munn 1998, Wirminghaus et al. 2001), although smaller parrot species may be active throughout the day (Pizo et al. 1997, Gilardi and Munn 1998). Survey data offer an approximation of activity patterns for a species at the population level, but may be limited by the varying detectability of individuals at certain times of the day, or biased toward above-canopy flight characteristics of large flocks. Direct techniques, such as radio-telemetry, offer the opportunity to follow an individual and track its behavior throughout the day, but these techniques have been used infrequently for parrots (Lindsey et al. 1991).

The Lilac-crowned Parrot (*Amazona finschi*) is a threatened species (Diario Oficial de

la Federación 2002) endemic to the Pacific slope of Mexico (Forshaw 1989). Observations of nesting Lilac-crowned Parrots demonstrate that breeding pairs make only two foraging visits to the nest per day: in the early morning and late afternoon (Renton and Salinas-Melgoza 1999). The Red-crowned Parrot (*Amazona viridigenalis*) in northeastern Mexico also makes only two foraging trips to the nest per day (Enkerlin-Hoefflich and Hogan 1997). It is unknown, however, whether these visits reflect general activity periods for parrots, or are specific to nesting pairs. We used radio-telemetry techniques to determine hourly activity patterns of individual Lilac-crowned Parrots in tropical dry forest during both the dry and the rainy seasons.

### METHODS

We conducted our study from 1996 to 2000 in the tropical dry forest of the 13,142-ha Reserva de la Biósfera de Chamela-Cuixmala (19° 22' N, 104° 56' W to 19° 35' N, 105° 03' W), Jalisco, on the Pacific coast of Mexico. The topography of the reserve is hilly, and is dominated by tropical dry deciduous forest with semi-deciduous forest in the larger drainages and more humid valleys (Lott 1993). Mean annual precipitation at the study site is 748 mm, with 85% of rainfall occurring from June to October; there is a prolonged drought from mid-February to late May (Bullock 1986). During 1996–2000, mean monthly temperatures were  $23.6 \pm 0.27^\circ\text{C}$  (SE) in the dry season (January–May), and  $26.9 \pm 0.33^\circ\text{C}$  in the rainy season (July–November).

We fitted radio-transmitters (model SI-2C; Holohil Systems, Carp, Ontario, Canada) onto

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Lilac-crowned Parrot chicks 10 days before fledging, permitting individuals to become accustomed to transmitter collars. Each radio-transmitter was encased in a brass cylinder with a 113-kg-test whip antenna, and crimped, copper tube attachments for the collar (Meyers 1996). Radio-collars weighed 11 g, corresponding to 3% of body weight (Kenward 1987, Renton 2002). Transmitter pulse rate was set at 0.6 p/sec, with a battery life of 12 months. We used TRX-1000S receivers (Wildlife Materials, Inc., Carbondale, Illinois), and located radio-collared parrots by triangulation of simultaneous readings from two of three, fixed telemetry stations (Nam and Boutin 1991). Each telemetry station was fitted with two 11-element, H-type antennas and a null-peak system (AVM, Inc., Isanti, Minnesota), providing a signal detection range of 10–15 km, with an error estimate of 1.4 degrees.

Over the 5 years of study, we obtained activity data on 29 juvenile parrots ( $n = 7, 4, 3, 12,$  and  $3$  parrots in 1996, 1997, 1998, 1999, and 2000, respectively). Activity readings of parrots were not determined until 1–2 months after fledging—once juveniles began moving with adult flocks and their behavior reflected that of adult birds (Salinas-Melgoza 2003). Telemetry sessions were conducted during both the rainy (July–November) and dry (January–May) seasons. Few telemetry sessions were conducted in December, and few successful telemetry sessions could be conducted in June due to seasonal migration of parrots out of the study site (Renton and Salinas-Melgoza 2002). Activity patterns were determined by conducting 13-hr telemetry sessions from the fixed stations, by recording the activity of individuals per hour after sunrise (approximately 06:30–19:30 [CST] in the dry season and 07:30–20:30 in the rainy season). Consecutive readings were taken in each hourly period to determine whether individuals changed location within the hour. Loss of signal with transmitter age and dispersal movements of parrots frequently made detection of individuals difficult; thus, not all telemetry sessions produced activity readings.

Transmitters did not have an activity sensor; therefore, the activity status of each individual was determined by maintaining the antenna in the peak signal direction and registering the level of signal intensity. An indi-

vidual was recorded as active when we registered fluctuations in signal intensity of  $>0.05$  dc milliamperes variation, caused by the individual changing position. We defined two activity categories: (1) rest: individuals with constant, unvarying signal intensity and no change in location or direction angle; and (2) active: individuals with a fluctuating signal intensity, or which changed location or signal direction. We recorded the number of individuals at rest or active during each hourly period, with the sum of the two categories being the total number of individuals recorded for that hour. To evaluate local movements involving flight, a subset of those individuals from the active category that registered a change in location or signal direction, was also defined as moving. Activity patterns were determined as the proportion of individuals per hour registered as active, as well as the subset of individuals in the active category that changed location and may be considered moving.

We used the Kolmogorov-Smirnov test of normality with Lilliefors significance correction (Zar 1999) to determine whether the data deviated significantly from the normal distribution required for parametric analysis. The proportions of individuals registered as active per hour in the dry and rainy seasons were arcsine transformed (Zar 1999) and presented a normal distribution ( $K-S_{26} = 0.13, P = 0.20$ ). We used a paired  $t$ -test to compare activity by hour after sunrise between the dry and rainy seasons. Arcsine-transformed proportions for the subset of individuals that changed locations were not normally distributed; therefore, the nonparametric Wilcoxon paired-sample test was used to compare movement between seasons, by hour after sunrise. Data are presented as means  $\pm$  SE; significance level was set at  $P < 0.05$ .

## RESULTS

Parrot activity was recorded for 845 hr of telemetry sessions, with 573 hr during the rainy season (July–November) and 272 hr in the dry season (January–May). Not all individuals could be recorded in all telemetry sessions, but we obtained 2,292 activity readings of individual juvenile parrots. Fewer telemetry sessions and activity readings were obtained during the dry season (505 readings) than in

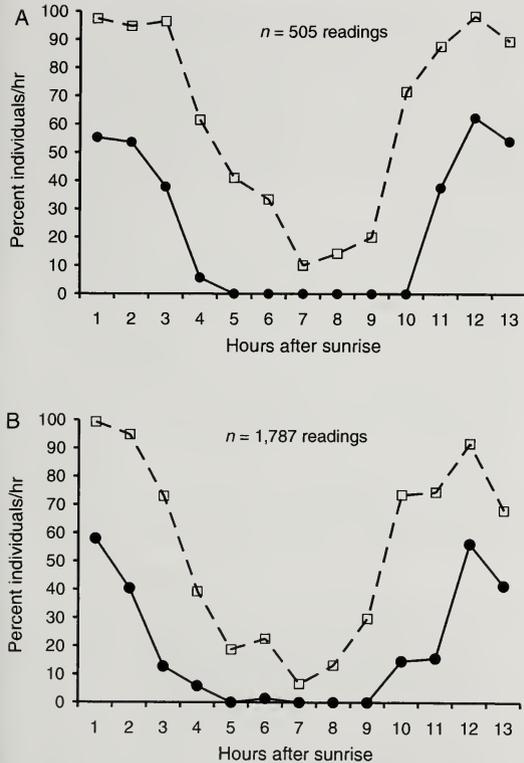


FIG 1. Percent of individual Lilac-crowned Parrots active (dashed line) and changing location (continuous line) per hour after sunrise in (A) the dry season and (B) the rainy season in the Reserva de la Biósfera de Chamela-Cuixmala, Jalisco, Mexico, 1996–2000.

the rainy season (1,787 readings), due to signal loss as transmitters aged and the broad dispersal of parrots during the dry season (Salinas-Melgoza 2003), which made detection difficult. Individuals were followed for  $271 \pm 27.6$  days (range = 55–552,  $n = 29$ ) until the battery died or the signal was lost. Most activity readings were of first-year juvenile parrots; only six individuals were followed >1 year, providing 117 readings that correspond to subadults 13–18 months of age.

Activity patterns of Lilac-crowned Parrots showed two peaks—both for overall activity and when changing location (Fig. 1). Peak activity of individuals occurred in the first 3–4 hr after sunrise and last 4 hr before sunset (Fig. 1), corresponding to the approximate time periods of 06:30–10:30 and 15:30–19:30 in the dry season, and 07:30–10:30 and 16:30–20:30 in the rainy season. Local movements of individuals changing location occurred in

the first 3 hr after sunrise and last 2 hr before sunset (Fig. 1), approximately 06:30 to 09:30 and 17:30 to 19:30 in the dry season, and 07:30 to 10:30 and 18:30 to 20:30 in the rainy season. During a large part of the day (11:00–16:00), parrots demonstrated low levels of activity and did not change location (Fig. 1). Peak periods in the early morning and late afternoon for active and moving individuals were similar in both the dry and rainy seasons. However, the percent of individuals active in the dry season (all-day mean =  $62.7\% \pm 9.57$ ) was greater than in the rainy season (all-day mean =  $54.2\% \pm 9.28$ ), with significant variation between seasons in the proportion of individuals active per hour of the day (paired  $t_{12} = 2.7$ ,  $P < 0.019$ ; Fig. 1). By comparison, the percent of individuals that changed location per hour of the day did not vary significantly between seasons (all-day mean for dry season =  $23.5\% \pm 7.33$ , rainy season =  $18.9\% \pm 6.12$ ;  $Z_{13} = 1.13$ ,  $P = 0.26$ ).

## DISCUSSION

Individual Lilac-crowned Parrots had two periods of peak activity—during the first 4 hr of the morning and the last 3 hr of the afternoon—when parrots are most likely to be foraging (Snyder et al. 1987). Peak movements of individuals in the early morning and late afternoon corresponded with the behavior of parrot flocks traveling between communal roost sites and foraging areas (Renton and Salinas-Melgoza 2002). Peak periods of activity and movements of individuals in the early morning and late afternoon make these the times of day when parrots are most likely to be detected during surveys, and correspond with the activity patterns estimated from survey data (Snyder et al. 1987, Gilardi and Munn 1998). Moreover, the same activity periods were observed for nesting parrots (Enkerlin-Hoeflich and Hogan 1997, Renton and Salinas-Melgoza 1999) and may reflect a general activity pattern irrespective of the age group or reproductive status of individuals.

Because Lilac-crowned Parrots are inactive for 5–6 hr of the day, periods of rest or activity by parrots need to be considered when using radio-telemetry data to evaluate habitat use. Habitat selected for resting likely differs from that for foraging because cover and security are more important when resting.

whereas food availability is more important when foraging (Palomares and Delibes 1992). Failure to take activity into account creates bias in estimates of habitat use, particularly for animals that spend part of the day inactive, because foraging habitat will be underestimated (Palomares and Delibes 1992).

The low activity exhibited by Lilac-crowned Parrots during part of the day may be related to diet, suggesting that parrots are able to meet their nutritional requirements by foraging during a few hours in the morning and afternoon. The Lilac-crowned Parrot is predominantly granivorous and exploits locally abundant seed resources (Renton 2001). Seeds are high in proteins and minerals (Gibaldi 1996) and require longer digestion periods, with consequently greater time between feeding sessions (Karasov 1990, Levey and Martínez del Río 2001). Frugivorous birds, by comparison, have rapid transit times of fruit in the gut, with a consequent increase in consumption rate (Levey and Karasov 1989, Martínez del Río and Restrepo 1993). Hence, granivorous Lilac-crowned Parrots may be able to meet their energetic needs in a few feeding bouts throughout the day.

The seasonal variation in activity levels of Lilac-crowned Parrots may be related to seasonal changes in food resource availability (Renton 2001). Decreased food availability in the dry season (Renton 2001) may require parrots to increase time spent foraging to obtain sufficient food resources. Anecdotal observations of parrots in the Australian wheat-belt suggest that parrots increase time spent foraging when food availability is low (Rowley 1990, Rowley and Chapman 1991). Average monthly temperatures also are greater in the rainy season than in the dry season and may influence parrots to seek cover or conserve energy by decreasing activity during the warmer months. However, we obtained fewer activity records of Lilac-crowned Parrots during the dry season than in the rainy season, because the broad dispersal of parrots during the dry season (Salinas-Melgoza 2003) made individuals more difficult to detect. By comparison, the pattern of changing locations did not vary between seasons, because these movements tend to reflect local flights between roosting and foraging sites—a consistent element of Lilac-crowned Parrot behavior.

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## PARROT NESTING IN SOUTHEASTERN PERU: SEASONAL PATTERNS AND KEYSTONE TREES

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**ABSTRACT.**—Parrots that inhabit tropical lowland forests are difficult to study, are poorly known, and little information is available on their nesting habits, making analysis of community-wide nesting patterns difficult. I present nesting records for 15 species of psittacids that co-occur in southeastern Peru. The psittacid breeding season in this area lasted from June to April, with smaller species nesting earlier than larger species. Why smaller species bred earlier is uncertain, though it may be related to interspecific competition for nest sites or variations in food availability. This study identified two keystone plant resources used by nesting parrots: *Dipteryx micrantha* (Fabaceae) and *Mauritia flexuosa* (Arecaceae). Local threats to these plant species are discussed. Received 25 August 2003, accepted 14 April 2005.

Nesting is a critically important stage in the natural history of all bird species. Reproductive failure has caused numerous conservation crises, so knowledge of nesting habits is critical (Ratcliffe 1967, Herkert et al. 2003). The nesting ecology of many tropical species remains poorly documented, especially for canopy nesters in dense, lowland tropical forests. The family Psittacidae is the most endangered large avian family in the world, making its study a conservation priority (Bennett and Owens 1997, Collar 1997). Most of our knowledge of parrot nesting comes from anecdotal accounts by early collectors (Huber 1933), regional avifaunal compendia (Cherrie 1916, Havershmidt 1968), detailed studies of individual taxa (reviewed in Masello and Quillfeldt 2002), and the monumental compendium of Forshaw (1989).

New World parrot diversity is highest in the western Amazon Basin, where communities commonly include more than 15 species (Roth 1984, Montambault 2002). This diversity peaks in southeastern Peru, where 18 to 20 species have been reported at various sites (Terborgh et al. 1984, Foster et al. 1994). However, the nesting season for all but five species in the region remains undocumented, making community-level analyses impossible. Here, I report on the nesting season for 15 species of sympatric parrots inhabiting lowlands of the western Amazon Basin in southeastern Peru.

Land clearing and pressures on global forest resources are constantly increasing. As for-

est areas shrink, conservationists must prioritize their conservation efforts. Large, old trees and the cavities they contain are vital for the persistence of many cavity-nesting birds (Mawson and Long 1994, Poulsen 2002). However, cavity nesters usually do not use trees in proportion to their abundance, suggesting that some tree species are more important than others to these birds (Martin and Eadie 1999, Monterrubio and Enkerlin 2004). In this study, I compiled nesting records for 15 species to determine which trees were most important to the nesting parrot community in southeastern Peru.

### METHODS

**Study area.**—I studied parrot nesting in the Departamento de Madre de Dios in southeastern Peru. The primary site was the Tambopata Research Center (13° 07' S, 69° 36' W; 250 m in elevation) on the border between the Tambopata National Reserve (275,000 ha) and Bahuaja-Sonene National Park (537,000 ha). The center is located in a small (<1 ha) clearing surrounded by a mix of mature floodplain forest, riparian successional forest, *Mauritia flexuosa* (Arecaceae) palm swamps, upland forest, and bamboo (Foster et al. 1994, Griscom and Ashton 2003; DJB pers. obs.). The forest is classified as tropical moist forest (Holdridge 1967). The site is adjacent to a 500-m-long, 30-m-high riverbank clay lick, where up to 1,000 macaws and parrots gather daily, resulting in high parrot densities in the area (Brightsmith 2004a). Annual rainfall is 3,200 mm. The dry season extends from April to October, during which monthly rainfall averages 90–250 mm (Brightsmith 2004a). Ad-

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ditional nesting records come from Posada Amazonas Lodge in the Native Community of Infierno (12° 48' S, 69° 18' W; 195 m in elevation; 2,800 mm annual rainfall; Pearson and Derr 1986, Brightsmith and Aramburú 2004) and Cocha Cashu Biological Station in Manu National Park (11° 54' S, 71° 18' W; 400 m in elevation; 2,000 mm annual rainfall; Terborgh 1983, Terborgh et al. 1984). These two sites are characterized by similar vegetation and dry seasons, and they are located 50 km north-northeast and 250 km northwest of Tambopata Research Center, respectively.

*Nesting records.*—Nesting records consisted of two types: confirmed nests and birds at cavities. Confirmed nests were locations where I observed eggs or chicks. Observations of birds at cavities, where contents were not checked, were included only when birds were observed repeatedly at the cavity and where behavioral cues suggested incubation or feeding of young. Single observations of birds at cavities were not included, as parrots may visit cavities when not breeding.

Most of the nesting records were from July to August (1998) and November to April (1999 to 2003) in Tambopata and September to November (1993, 1995, 1996, and 1997) in Manu. I collected additional unpublished nesting records from researchers and guides with experience working in southeastern Peru. These other observers were stationed at Tambopata year-round.

*Data analysis.*—I tested the relationship between body size and the onset of breeding using a rank correlation of body mass versus month of first breeding and a *t*-test ( $\alpha = 0.05$ ) of month of first breeding for large (>250 g) versus small (<250 g) psittacids (Gibbons 1985). Body-mass data are from Dunning (1993).

## RESULTS

*Red-and-green Macaw (Ara chloroptera).*—Twelve nests of this species were monitored in Tambopata between 1993 and 2003. I determined laying date for nine nests: September ( $n = 1$ ), November ( $n = 7$ ), and December ( $n = 1$ ). Fledging was confirmed in January ( $n = 1$ ) and March ( $n = 5$ ; Table 1). Most nests were in cavities of live, emergent *Dipteryx* (Fabaceae) trees ( $n = 7$ ), although one nest was in a cavity of an unidentified

tree. One pair, consisting of a wild bird and a hand-raised bird released to the wild, nested in wooden nest boxes in 2 years (see Nycander et al. 1995 for a description of the nest boxes). Three nests were in floodplain forest (one <10 m from the river edge) and nine were in *terra firme* forest.

*Blue-and-yellow Macaw (Ara ararauna).*—Seventy-two nests in at least 50 different cavities were recorded. Most cavities (47 of 50) were in dead *Mauritia flexuosa* palms. Because it is difficult to climb dead palms, only 21 nest trees were climbed, and nest contents were checked infrequently. I estimated that egg laying occurred in November ( $n = 9$ ), December ( $n = 2$ ), and January ( $n = 2$ ). I confirmed fledging in late February ( $n = 1$ ), March ( $n = 4$ ), and May ( $n = 1$ ). Fifty of these nests were in a 3-ha section of naturally dying *Mauritia flexuosa* palm swamp, where dead palms occurred at a density of >200 per ha (A. Bravo and DJB unpubl. data). Sixteen nests were in a small (<0.25 ha) section of a swamp being managed to encourage nesting of Blue-and-yellow Macaws (Nycander et al. 1995). Three other nests were in tall, dead palms that rose above the surrounding vegetation in an otherwise healthy palm swamp. Two nests were in floodplain forest in dead *Iriartea* palms <10 m from the river edge. One additional nest was in an unidentified dead, hollow tree in *terra firme* forest, 10 m from the edge of a cliff that overlooked the Tambopata River. The cavity was a deep, open-topped tube, similar in structure to a hollow palm.

*Scarlet Macaw (Ara macao).*—I studied 55 clutches at 26 different nest sites. I was certain of first-clutch initiation for 40 nests: late October ( $n = 1$ ), November ( $n = 32$ ), and December ( $n = 7$ ). When the first clutch was lost or did not hatch, 35% (7 of 20) of the birds re-laid in the same nest. Second clutches were initiated in late December ( $n = 4$ ) or early January ( $n = 3$ ). Fledging took place in February ( $n = 4$ ), March ( $n = 14$ ), and April ( $n = 2$ ). No eggs from second clutches hatched. Nests were found in natural cavities of live *Dipteryx micrantha* ( $n = 6$ ), live *Hymenaea oblongifolia* (Fabaceae;  $n = 1$ ), dead *Iriartea* palm ( $n = 1$ ), and in artificial nest boxes made of wood or PVC pipe ( $n = 18$ ). No nests were found in dead *Mauritia* palms. Nests were in

floodplain forest ( $n = 15$ ), *terra firme* forest ( $n = 9$ ), and *Mauritia* palm swamp ( $n = 1$ ); the habitat for one nest was not recorded.

*Chestnut-fronted Macaw* (*Ara severa*).—Birds were observed attending seven cavities from November to February (Table 1). Observers saw the nest contents in only one cavity; the nest was in a dead *Mauritia flexuosa* palm in the dying section of swamp discussed under Blue-and-yellow Macaw. It contained chicks in February. The other nests were in canopy branches of emergent *Dipteryx micrantha* trees ( $n = 6$ ). All of the nest cavities were in trees that were relatively isolated from the surrounding vegetation in *terra firme* forest ( $n = 4$ ), floodplain forest ( $n = 2$ ), or *Mauritia* palm swamp ( $n = 1$ ).

*Red-bellied Macaw* (*Orthopsittaca manillata*).—I observed birds attending 26 cavities in Tambopata from October to February. Four nests contained eggs or chicks, and I estimated that eggs were laid in October ( $n = 2$ ) and November ( $n = 2$ ). All nests were in dead *Mauritia flexuosa* palms; three nests were in the small (<0.25 ha) section of managed palm swamp, and 22 nests were in the 3-ha section of naturally dying *Mauritia flexuosa* swamp. Both habitats are described above in the section on Blue-and-yellow Macaw.

*White-eyed Parakeet* (*Aratinga leucophthalmus*).—In January, my assistants observed birds repeatedly attending a cavity in a dead palm in the center of a farm field. The pair was likely incubating or brooding because one bird entered the palm and refused to leave, even when observers knocked on the trunk of the palm.

*Dusky-headed Parakeet* (*Aratinga weddellii*).—No chicks of this species were seen; all three records reported here are of birds attending cavities in dead trees or dead branches in live trees. The reports from Tambopata come from July, December, and January. These observations are congruent with a report from local residents who say that the species nests “year-round” (Sixto Duri pers. comm.). Nest cavities were in a dead tree of an unknown species ( $n = 1$ ), a dead palm ( $n = 1$ ), and a dead branch in a live *Cecropia* (Cecropiaceae) tree ( $n = 1$ ). The nesting habitats included river edge ( $n = 1$ ), small farm ( $n = 1$ ), and a large natural gap in *terra firme* forest ( $n = 1$ ).

*Scarlet-shouldered Parrotlet* (*Touit huetii*).—This species is rare at the study sites. From August to September 1998, guides and guests at Tambopata Research Center repeatedly saw two birds at a hole in an arboreal termite mound 3.5- to 4-m above the ground. The site was in *terra firme* forest with a mix of trees and bamboo (*Guadua sarcocarpa*). The birds were seen regularly attending the cavity over a period of a few weeks.

*Red-crowned Parakeet* (*Pyrrhura roseifrons*).—I located one nest of this species during October 1997 in Manu National Park. The nest was approximately 9 m high in a live tree in late-successional floodplain forest. One newly hatched chick and three eggs were seen on 4 October. A total of four birds attended this nest. They appeared to be adults, although two of the birds had less red on the head and may have been young from the previous year. During my last visit to the nest (4 November), I heard young birds begging inside the cavity.

*White-bellied Parrot* (*Pionites leucogaster*).—Two live featherless chicks were found at the base of a suspected nesting tree in October, indicating that eggs were laid in August; fledging would have occurred in November or early December. Birds were seen attending three additional cavities in Tambopata and Manu from September to February. The nest cavities were in canopy branches of live trees (two *Dipteryx micrantha* and one unknown species).

*Blue-headed Parrot* (*Pionus menstruus*).—Five nests of this species were found, all from June to November (Table 1). Laying dates were calculated for two nests: late May or early June ( $n = 1$ ) and September ( $n = 1$ ). Chicks were seen in three nests. Fledging in November was confirmed at one nest. Nest sites were dead palms ( $n = 2$ ) and PVC nest boxes ( $n = 2$ ). All nests were near some sort of forest edge: river edge ( $n = 2$ ), clearing edge ( $n = 1$ ), and a steep drop-off in *terra firme* forest ( $n = 1$ ). Habitat was not recorded for one nest.

*Yellow-crowned Parrot* (*Amazona ochrocephala*).—A member of this species was seen attending a dead palm from at least December to March in mature floodplain forest (A. del Campo pers. comm.). However, local people report that the chicks of this species fledge in October. Birds were also seen briefly at three

TABLE 1. Parrot nesting phenology, by month and by season (dry or wet), in southeastern Peru (Departamento de Madre de Dios), 1993–1999. An “X” indicates peak breeding season (and chicks or eggs seen in the nest), “o” indicates periods when few birds breed, and “C” indicates that birds were observed regularly attending cavities (but no eggs or nestlings observed).

Species	Mass <sup>a</sup>	Dry season						Wet season						Dry season		
		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May			
Red-and-green Macaw ( <i>Ara chloroptera</i> )	1,250				o	o	X	X	X	X	X	X	X			
Blue-and-yellow Macaw ( <i>Ara ararauna</i> )	1,125						X	X	X	X	X	X	X			
Scarlet Macaw ( <i>Ara macao</i> )	1,015					o					X	X	X		o	o
Mealy Parrot ( <i>Amazona farinosa</i> )	610										X	X	X			
Yellow-crowned Parrot ( <i>Amazona ochrocephala</i> )	510										C	C	C			
Chestnut-fronted Macaw ( <i>Ara severa</i> )	430										X	X	X			
Red-bellied Macaw ( <i>Orthopsittacus manilata</i> )	370									X	X	X	X			
Blue-headed Parakeet ( <i>Pionus menstruus</i> )	247	X	X		X	X										
White-eyed Parakeet ( <i>Araitinga leucophthalmus</i> )	157															
White-bellied Parrot ( <i>Pionites leucogaster</i> )	155				X	X					C	C	C			
Dusky-headed Parakeet ( <i>Araitinga weddellii</i> )	108		C													
Cobalt-winged Parakeet <sup>b</sup> ( <i>Brotogeris cyanoptera</i> )	67			X	X	X	X									
Red-crowned Parakeet ( <i>Pyrrhura roseifrons</i> )	65				X	X	X									
Scarlet-shouldered Parrotlet ( <i>Touit huetii</i> )	60			C	C											
Tui Parakeet <sup>b</sup> ( <i>Brotogeris sanctithomae</i> )	59			X	X	X	X									

<sup>a</sup> Mass data from Dunning (1993).

<sup>b</sup> Nest data from Brightsmith (2004b).

other cavities in floodplain forest (*Dipteryx micrantha*, *Erythrina* sp. and an unknown species; A. del Campo and J. I. Rojas pers. comm.).

*Mealy Parrot (Amazona farinosa)*.—I observed two nests of this species. Eggs were laid in December ( $n = 1$ ) and January ( $n = 1$ ). Both nests were in floodplain forest; one had two eggs, the other one egg and one chick. One was in a dead *Iriartea* palm, the other in a natural cavity in a live emergent *Dipteryx micrantha* tree.

*Relationship between body size and breeding season*.—Most parrots and parakeets bred from June to November, whereas the macaws, Mealy Parrot, and White-eyed Parakeet nested from November to March (Table 1). Smaller parrot species initiated nesting significantly earlier in the season than larger parrots. This trend held for all 15 species (rank correlation:  $r = 0.70$ ;  $t$ -test:  $t = 3.08$ ,  $df = 13$ ,  $P = 0.009$ ; species listed in Table 1) and for the 11 species of which I observed chicks or eggs (rank correlation:  $r = 0.81$ ;  $t$ -test:  $t = 5.25$ ,  $df = 9$ ,  $P < 0.001$ ). I was unable to analyze body size versus nesting season using only phylogenetically independent contrasts because there is no complete phylogeny of New World parrots (Wolf et al. 1998, Tavares et al. 2004). However, the available partial phylogenies show that there are at least two independent comparisons in the data set: Red-bellied Macaw versus Blue-and-yellow Macaw and Blue-headed Parrot versus Mealy Parrot (Russello and Amato 2003, Ribas and Miyaki 2004). In both cases, the smaller species nests first.

## DISCUSSION

During this study, nests or suspected nest sites were found for 13 of the 20 species of psittacids. This includes the first nest-site description for Scarlet-shouldered Parrotlet and the second for White-bellied Parrot. For White-bellied Parrot, the only previous nesting record is of an incubating female in a tree cavity in eastern Brazil (Forshaw 1989). Of the seven psittacid species for which nests were not discovered, previous nest data are available for three. In Manu National Park, Cobalt-winged Parakeet (*Brotogeris cyanoptera*) and Tui Parakeet (*B. sanctithomae*) both nest in termite mounds, lay eggs in August and September, and have chicks from mid-

September to mid-November (Brightsmith 2000, 2004b). Amazonian Parrotlets (*Nannopsittaca dachilleae*) in Tambopata attended a tree cavity in July and September (O'Neill et al. 1991). Of the remaining four species, none has been found nesting in the region: Dusky-billed Parrotlets (*Forpus sclateri*) were seen going in and out of a tree cavity in July in northern Peru (Forshaw 1989). No nests have been reported for Orange-cheeked Parrots (*Pionopsitta barrabandi*), but sightings of recently fledged young of this species at the Tambopata clay lick in December and February suggest that the birds may lay eggs in October or earlier (DJB pers. obs.). In Brazil, recently fledged Orange-cheeked Parrots also were seen during February and early March (Roth 1984, Forshaw 1989). No nesting information is available for Black-capped Parakeet (*Pyrrhura rupicola*) or Blue-headed Macaw (*Procyrrhura couloni*; Forshaw 1989, Collar 1997, Juniper and Parr 1998).

The finding that smaller species bred earlier was unexpected, but it could be related to interspecific competition for nest sites or variations in the availability of food resources (Roth 1984). Competition between species is potentially important because Chestnut-fronted Macaws, Mealy Parrots, Yellow-crowned Parrots, toucans (*Ramphastos* spp.), Scarlet Macaws, and Red-and-green Macaws all overlapped in their nest-site preferences (DJB unpubl. data). However, most of the smaller species that nested early in the season used substrates and cavities ignored by larger birds (e.g., termite mounds, thin dead palms, and small cavities; DJB pers. obs.) suggesting that something other than just competition drives the nesting phenology patterns I observed.

Seasonal differences in nesting may be due to differences in diet and food availability. The smaller parrots that nest in the dry season usually eat more nectar, flowers, and small seeds than larger species (Roth 1984, Desenne 1994; see also Terborgh 1983 for similar patterns exhibited by primates). Flowering in many tropical communities peaks in the dry season (van Schaik et al. 1993, Fenner 1998) and many wind-dispersed plants fruit in the dry season, when deciduous canopy trees lose their leaves and higher wind velocities produce ideal dispersal conditions (Fenner 1998). Because flowers and small wind-dispersed

seeds are relatively low-quality foods that require a large energy investment to harvest, smaller-bodied parrots should have an advantage when exploiting these resources (Terborgh 1983). As a result, larger species should incur comparatively greater food shortages in the dry season than smaller species, explaining the wet season breeding of larger parrots found in Tambopata. Notably, the earliest-breeding species was the mid-sized Blue-headed Parrot; members of its genus (*Pionus*) are known to eat many flowers (Galetti 1993).

Nest searching was not conducted with equal intensity in all months. Although sampling efforts were more intense later in the season, most of my nesting records for small species come from the early part of the season. I have had crews observing macaws continuously from November 2000 to May 2004, and they did not witness large macaws nesting earlier in the season. Conducting more nest searches from May through August would likely reveal additional small species breeding, corroborating the trend we found.

Few studies have addressed parrot nesting seasonality at the community level. Roth (1984) hypothesized that congeners staggered breeding to avoid competition for food. His data support the pattern for *Aratinga* and *Amazona*, where smaller species did nest earlier, but *Pyrhura* and *Ara* overlapped extensively. My data, however, do not support temporal spacing by congeners, and my analysis of Roth's (1984) data shows that smaller species tended to nest earlier, but not significantly so (rank correlation:  $r = 0.34$ ;  $t$ -test:  $t = 0.94$ ,  $df = 12$ ,  $P = 0.37$ ). Future studies should investigate the interplay of competition for nest sites, diet, and phenological cycles in determining the seasonality of parrot breeding.

My study highlighted two types of sites that are very important to nesting parrots: emergent *Dipteryx micrantha* trees and dead palms. Six species were recorded using large, emergent *Dipteryx micrantha* trees, and 75 and 88% of the natural nests used by Scarlet and Red-and-green macaws, respectively, were in these trees (see also Nycander et al. 1995). Large emergents of this species often contained dozens of cavities, and individual trees often had multiple pairs of macaws nesting in them simultaneously (A. Hepworth and DJB unpubl. data). Because *Dipteryx micrantha*

can live for over 1,000 years, cavities in these trees may remain useable by macaws for decades or centuries (Chambers et al. 1998; but see Fichtler et al. 2003). As a result, hundreds of macaw chicks may be produced from a single tree during its lifetime. The fruits of *Dipteryx* species are also a keystone resource for a variety of tropical frugivores and granivores, including Great Green Macaws (*Ara ambigua*; G. Powell unpubl. data), bats (*Artibeus* spp.; Romo 1997), squirrels (*Sciurus* spp.), and agoutis (*Dasyprocta* spp.; Emmons 1984, Forget 1993)

Unfortunately, *Dipteryx* trees are increasingly logged throughout their range. *Dipteryx* wood is in high demand for hardwood flooring (Toledo and Rincón 1999, Wood Flooring International 2003) and, in Peru, people use the wood to make charcoal. Landowners sell trees >1 m in diameter for as little as US \$30 (A. Hepworth unpubl. data). The recent increased harvest of *Dipteryx panamensis* in Costa Rica is the most probable cause for the precipitous decline of Great Green Macaws in that country (Bjork and Powell 1995, Chassot and Monge 2002). Management schemes involving planting of *Dipteryx* trees are underway in Costa Rica. This can produce fruiting trees, but large, gnarled adult trees riddled with useable cavities are practically irreplaceable, as they take hundreds of years to grow.

Palms have long been recognized as vital to the survival of tropical frugivores and granivores (Emmons 1984, Henderson 1995). In fact, several New World parrots are thought to be almost completely dependent on palms for food, nesting sites, or both (Yamashita 1987, Forshaw 1989, Yamashita and Valle 1993, Yamashita and Barros 1997, Salaman et al. 2001). Eight parrot species were observed nesting in palms during this study, and reports from the literature show that two additional species also use palms (Red-and-green Macaw and Dusky-headed Parakeet; Forshaw 1989, Nycander et al. 1995). In sum, half of the parrot species in this community nest in palms and palms are important not only for specialists, but for many generalists as well.

*Mauritia flexuosa* palms are particularly valuable resources for parrots (Forshaw 1989, Bonadie and Bacon 2000). In Peru, at least seven species of psittacids nest in *Mauritia* palms (González 2003; this study), and studies

on Trinidad show that palm swamps are key to the maintenance of parrot populations (Bonadie and Bacon 2000). Dying palm swamps are particularly valuable because parrots nest at high densities in these sites. González (2003) reported aggregations of macaws in dying sections of *Mauritia* palm swamps in northern Peru, similar to what I report for Tambopata. Nesting densities there (0.075 nests/ha; range = 0.038–0.128/ha) were 100× smaller than those in Tambopata (>29 nests in 3 ha or >9.7/ha). In northern Peru, the parrots spread out over larger areas of dying swamp, and parrot collectors regularly reduced the nest densities (González 2003). In Tambopata, the birds were concentrated in a small, protected area near a large clay lick (Brightsmith 2004a). Breeding near the clay lick may be particularly important because adult parrots feed their nestlings clay and concentrate their use of the lick during the breeding season (DJB unpubl. data).

Areas of palm swamp can die synchronously in response to flooding and other events that result in depositions of large sediment loads (Kahn 1988, González 2003; DJB pers. obs.). How long the dead palms remain useable for nesting parrots under natural conditions is unknown. However, *Mauritia* palms that died when their tops were cut off remained upright an average of 4 to 5 years before they fell (Nycander et al. 1995; DJB unpubl. data). The short, useful lifetime of individual dead palms suggests that dying palm swamps slowly shift in the landscape as new areas die and old areas become unusable. Like most parrots, those that nest in these dead swamps probably “wander,” tracking shifts in food resources and nest-site availability (Collar 1997, Renton 2002). As a result, dying palm swamps probably serve as breeding “source” areas in landscape-level source-sink dynamics and play a disproportionately large role in maintaining regional populations of these long-lived and highly mobile psittacids.

Palms are valuable to local people, and dozens of species are used for food, fiber, construction materials, fuel, and medicines (Vásquez and Gentry 1989, Henderson 1995). Overexploitation is common and its potential impact on the ecosystem is great (Johnson 1986, Bonadie and Bacon 2000). *Mauritia flexuosa* swamps cover at least 2 million ha in

the Iquitos region alone, but they are threatened because local people commonly cut entire trees to harvest weevil larvae (*Dryophthoridae: Rhynchophorus palmarum*) and fruit (Peters et al. 1989, Vasquez and Gentry 1989). However, many psittacids, game species, and large-bodied seed dispersers that move between the swamps and the surrounding landscape also depend on these fruits (Bodmer 1990, Bonadie and Bacon 2000). As a result, the loss of these swamps would have great impacts on the ecosystem.

The two primary nesting resources exploited by parrots in southeastern Peru are structurally different. In fact, they represent opposite ends of the tree-cavity spectrum. The dead palms are hollow tubes with open tops that allow rain to enter. They are thin-walled, poorly insulated, and flimsy; also, they last for only a few years before collapsing. In comparison, *Dipteryx* cavities have thick walls of hard wood, full roofs that provide protection from the rain, and are usually in live sections of solid trees that live for centuries (Chambers et al. 1998; DJB pers. obs.). It is surprising that two such different substrates attracted the majority of nesting parrots. The only characteristic they shared was their isolation from the surrounding vegetation. Dead-palm nest sites were almost always in the open: along river edges, in dead swamps, above the surrounding canopy, or in forest openings. The *Dipteryx* cavities were far from heavy epiphyte and vine cover, distant from adjacent trees, and high above the ground. This suggests that protection from non-volant predators has a great influence on parrot nest-site selection (Massello and Quillfeldt 2002, Brightsmith 2005a, 2005b).

The availability of suitable nest sites limits the reproductive output of many cavity-nesting species, especially in anthropogenically modified landscapes (Newton 1994). This study suggests that *Dipteryx micrantha* and *Mauritia flexuosa* are keystone tree species for parrots nesting in southeastern Peru. Clearing for agriculture, targeted destruction of parrot nests by collectors, and selective felling of key tree species will reduce the density of suitable nest cavities. Future studies should continue to identify key nesting resources for parrots and other cavity-nesting species so

that these important habitat features can be conserved in tropical landscapes.

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## GROUP-SIZE EFFECTS AND PARENTAL INVESTMENT STRATEGIES DURING INCUBATION IN JOINT-NESTING TAIWAN YUHNAS (*YUHINA BRUNNEICEPS*)

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**ABSTRACT.**—We investigated the effect of group size on incubation effort in Taiwan Yuhinas (*Yuhina brunneiceps*) at the Highlands Experimental Farm of National Taiwan University at Meifeng, Nantou County, central Taiwan, during 2000 and 2001. The Taiwan Yuhina is a joint-nesting, cooperatively breeding species endemic to Taiwan. We compared differences in parental investment among individuals of different sexes and status, explored the effect of group size on group incubation effort, and investigated whether individuals show compensatory reductions in care with respect to the number of females laying. Constancy of incubation increased as group size increased. Alpha females exhibited a significantly greater incubation effort than other individuals, but effort was similar among other group members. Both alpha males and females decreased their relative and absolute incubation effort as group size increased (i.e., there was a compensatory reduction in parental effort). However, beta pairs maintained a consistent but low incubation effort when either gamma pairs or an extra individual joined the group. Our study also demonstrated a new potential group-size benefit for cooperatively breeding birds—an increase in the constancy of incubation. Received 6 July 2004, accepted 31 March 2005.

The effect of group size on individual fitness is one of the most important aspects in understanding the evolution of sociality (Brown 1983, Kokko et al. 2001). In cooperatively breeding animals, individuals share parental effort with other group members. The optimal parental investment of each individual depends largely on the sum of other group members' parental efforts; that is, parental effort is affected by group size. Much attention has been paid to how individual provisioning effort is affected by group size in helper-at-the-nest systems (Hatchwell 1999). Two types of provisioning effort are recognized: additive and compensatory (Hatchwell 1999). Additive provisioning occurs when parents maintain the same provisioning effort, regardless of the number of helpers; thus, the total provisioning rate increases as group size increases (Emlen and Wrege 1991). On the other hand, compensatory provisioning occurs when total effort is comparatively constant and breeding individuals reduce their parental effort in response to increasing levels of effort by helpers (Brown et al. 1978). In a detailed comparative

study, Hatchwell (1999) showed that (1) care tends to be additive when the probability of nestling starvation is high and (2) parents are more likely to show compensatory reductions in care when the chance of starvation is low. In addition, Hatchwell hypothesized that male breeders may tend to exhibit compensatory reductions due to the uncertainty of parentage.

Little research has been conducted on the parental investment strategies of cooperative breeders during incubation (Vehrencamp 1977, Heinsohn and Cockburn 1994, Komdeur 1994). Mammalian studies have demonstrated that variation in the relative contributions of individual helpers to different cooperative activities, such as nursing and guarding, is important (Clutton-Brock et al. 2003). Incubation is certainly an important component of reproductive success in most bird species and has been considered a costly behavior (Visser and Lessells 2001, Reid et al. 2002b). Incubation among cooperative breeders is especially interesting to study because—in contrast to the cues received from nestlings—parents and helpers receive no cues from the eggs as to how much care is being given by other group members.

We investigated the effect of group size on incubation effort in a joint-nesting passerine, the Taiwan Yuhina (*Yuhina brunneiceps*, hereafter referred to as yuhina). Our study focused on whether additive and compensatory investment strategies, developed in the context

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of nestling provisioning, are also applicable to incubation effort. We explicitly considered two issues. First, we explored the effect of group size on total incubation effort. Second, we investigated whether individuals exhibited compensatory reductions in care by comparing the differences in parental investment strategies between individuals of different sex and status with respect to the number of breeding pairs.

## METHODS

*Study population.*—The Taiwan Yuhina, a Timaliine babbler, is endemic to Taiwan (Clements 2000). Since Yamashina (1938) first described the species' communal nesting behaviors, there has been no detailed study of this species. We have been studying a color-banded population of Taiwan Yuhinas since 1995 at the Highlands Experimental Farm of National Taiwan University at Meifeng, Nantou County, central Taiwan (24° 05' N, 121° 10' E; 2,150 m in elevation). During June 2000, average daytime and nighttime temperature was 25.2°C and 12.2°C, respectively. The study site has been described in detail elsewhere (Yuan et al. 2004). The yuhinas' breeding season lasts 6 months, usually from March or April to August or September. Yuhinas build open-cup nests 1–15 m above ground in various substrates along forest edges. Most juveniles (78%) disappear from the study area after their hatch year; therefore, most (92%) new group members are not closely related. Breeding groups comprise one to three monogamous pairs (mode = 2 pairs) and sometimes one extra male. Within each group, there is a linear hierarchy of socially monogamous pairs with all pairs contributing some eggs. The combined clutch size increases as group size increases. However, the average number of eggs laid by each female decreases with increasing group size (Yuan et al. 2004). According to data from microsatellite genetic markers, mean reproductive skew (the partitioning of reproduction among same-sex individuals within social groups) is low (Yuan et al. 2004), and all breeding pairs contribute to nest building, incubation, and provisioning (H-WY unpubl. data).

Alpha and beta individuals were identified by observing chasing and displacement behavior among group members. Particular in-

dividuals—both males and females—consistently chased and displaced same-sex members of their group. In larger groups, gamma individuals were chased by both alpha and beta individuals (see Yuan et al. 2004 for further details). Sex of all banded individuals (97% of the birds that we observed were color-banded) was assigned tentatively in the field based on observations of singing and copulation; later, gender was verified against sex-specific genetic markers via PCR (Fridolfsson and Ellegren 1999).

*Incubation.*—We observed diurnal incubation bouts from blinds 10–15 m from nests by using 15 × 40 image-stabilized binoculars. We recorded incubation effort at 21 nests of 11 breeding groups from June to August in 2000 and from March to August in 2001. The mean total observation time for each nest was 683 min (range = 252–1,096 min) and the mean continuous observation period was 414 min (range = 235–839 min). We successfully identified most individuals ( $89 \pm 2.4\%$ ) involved in incubation at each nest. We observed incubation effort during the first 10 days of the incubation period (mean = 5.69 days  $\pm$  2.33 SD of observation per nest).

*Data analysis.*—Constancy of incubation (i.e., the time that the eggs are in contact with any adult bird, expressed as the percentage of time eggs were incubated; Deeming 2002) differed from nest to nest. A mixed model was originally used to deal with the problem of repeated measurement of different nest attempts within the same group. However, because "group" (indicating different breeding group) had a negative component of variance, the mixed model was equivalent to GLM in this case (Schall 1991); therefore, GLM was used.

Individual incubation effort was assessed in two ways: as relative incubation effort (RIE) and as absolute incubation effort (AIE). We calculated RIE by dividing each individual's incubation time by the group's total incubation time. We calculated AIE by dividing each individual's incubation time by total observation time (group's total incubation time + time during which nest was unattended). We analyzed individual incubation effort (RIE and AIE) by using the residual maximum likelihood (REML) algorithm (mixed model) in SPSS 12.0 (SPSS, Inc. 2003) with normal er-

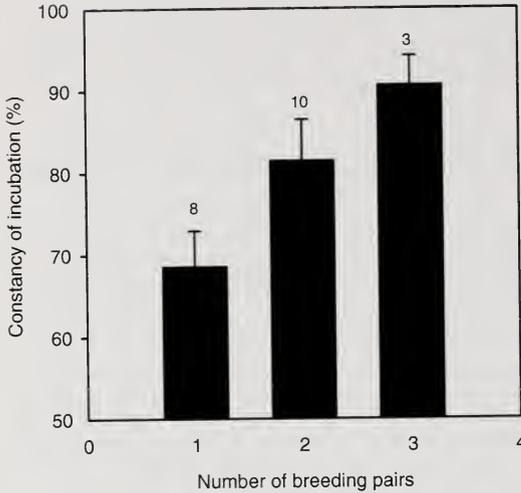


FIG. 1. Relationship between group size (number of breeding pairs) and incubation constancy for Taiwan Yuhinas in Nantou County, central Taiwan, 2000–2001. Larger groups had significantly greater constancy of incubation than smaller groups. Error bars are  $\pm$  SE. Sample size (number of nests) shown above bars.

ror structures, in which both fixed and random terms can be fitted. Random terms control for the use of repeated measurements within a given group, nest (different nest attempts of each group), pair status (i.e., alpha, beta, and gamma birds, and extra males without mates in odd numbered groups), and sex. However, the only interaction term we used in the analysis of alpha's and beta's incubation effort was "group"  $\times$  "status" because all other factors had a negative component of variance (Schall 1991). The incubation effort of gamma pairs and extra males were excluded in all analyses due to their small sample sizes. However, gamma pairs affected group size and "extra" was used as a categorical variable to see if an extra male would affect other individuals' incubation effort. Least significant difference (LSD) post hoc pairwise comparisons were used to compare individual effort for each sex and social rank.

Given that sex and status had a significant interaction effect, we also use a mixed model REML to analyze factors affecting alpha pairs' and beta pairs' incubation efforts separately. However, group fitted as the random term had a negative component of variance, so the mixed model is equivalent to GLM in this analysis. We report means  $\pm$  SE through-

TABLE 1. Results from a mixed model (residual maximum likelihood, REML) of relative incubation effort (RIE) for breeders of alpha and beta pairs of Taiwan Yuhinas in Nantou County, central Taiwan, 2000–2001.

Effect	df	F	P
Intercept	1, 8	15.59	0.004
Sex	1, 34	4.21	0.048
Status	1, 8	5.94	0.040
Group size	1, 7	1.89	0.21
Sex $\times$ status	1, 34	4.68	0.038
Status $\times$ group size <sup>a</sup>	1, 8	2.99	0.12
Sex $\times$ group size	1, 34	1.53	0.23
Extra $\times$ group size	1, 6	0.09	0.77

<sup>a</sup> Status  $\times$  group size was included in the model as a random factor. Estimate of variance =  $33.90 \pm 46.37$  (SE).

out this paper. All tests are two-tailed, with a significance criterion of  $P < 0.05$ .

## RESULTS

*Factors influencing constancy of incubation and individual contributions to incubation.*—Constancy of incubation (% of time eggs were incubated) was significantly influenced by group size (GLM,  $F_{1,21} = 7.32$ ,  $P = 0.014$ ; Fig. 1), but not by month of breeding ( $F_{1,21} = 0.20$ ,  $P = 0.25$ ), number of previous nesting attempts ( $F_{1,21} = 0.297$ ,  $P = 0.59$ ), or days after first incubation ( $F_{1,21} = 0.475$ ,  $P = 0.50$ ). Individual RIE differed between sexes (group sizes combined, alpha and beta birds combined:  $23.13 \pm 2.38\%$  for males,  $35.64 \pm 3.64\%$  for females) and status class (group sizes combined, males and females combined:  $36.34 \pm 2.91\%$  for alpha birds,  $17.63 \pm 2.33\%$  for beta birds), and there was a significant sex  $\times$  status interaction (Table 1). AIE did not differ between the sexes ( $P = 0.18$ ) or between birds of different status ( $P = 0.11$ ), but there was a significant interaction between sex and status (Table 2). Pairwise comparisons show that alpha females contributed more than all other birds in RIE (group sizes combined): alpha female ( $45.73 \pm 3.93\%$ ) versus alpha male ( $26.94 \pm 3.23\%$ ,  $P < 0.001$ ); alpha female versus beta female ( $18.28 \pm 3.87\%$ ,  $P < 0.001$ ). Alpha females also contributed more than all other birds in AIE (group sizes combined): alpha female ( $34.16 \pm 2.54\%$ ) versus alpha male ( $20.22 \pm 2.44\%$ ,  $P < 0.001$ ); alpha female versus beta female ( $15.92 \pm 3.35\%$ ,  $P = 0.001$ ). There

TABLE 2. Results from a mixed model (residual maximum likelihood, REML) of absolute incubation effort (AIE) for breeders of alpha and beta pairs of Taiwan Yuhinas in Nantou County, central Taiwan, 2000–2001.

Effect	df	F	P
Intercept	1, 6	10.87	0.018
Sex	1, 28	1.91	0.18
Status	1, 5	3.74	0.11
Group size	1, 5	0.20	0.67
Sex × status	1, 28	4.37	0.046
Status × group size <sup>a</sup>	1, 5	1.63	0.26
Sex × group size	1, 28	0.40	0.53
Extra × group size	1, 3	0.48	0.54

<sup>a</sup> Status × group size was included in the model as a random factor. Estimate of variance = 17.02 ± 30.77 (SE).

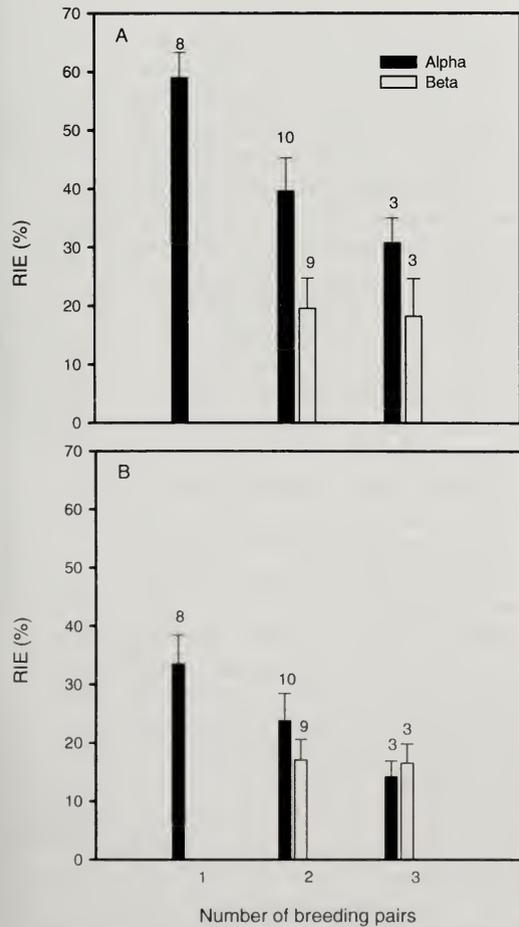


FIG. 2. Mean (± SE) relative incubation effort (RIE) of (A) females and (B) males in different group sizes (number of breeding pairs) of Taiwan Yuhinas in Nantou County, central Taiwan, 2000–2001. Sample size (number of nests) shown above bars.

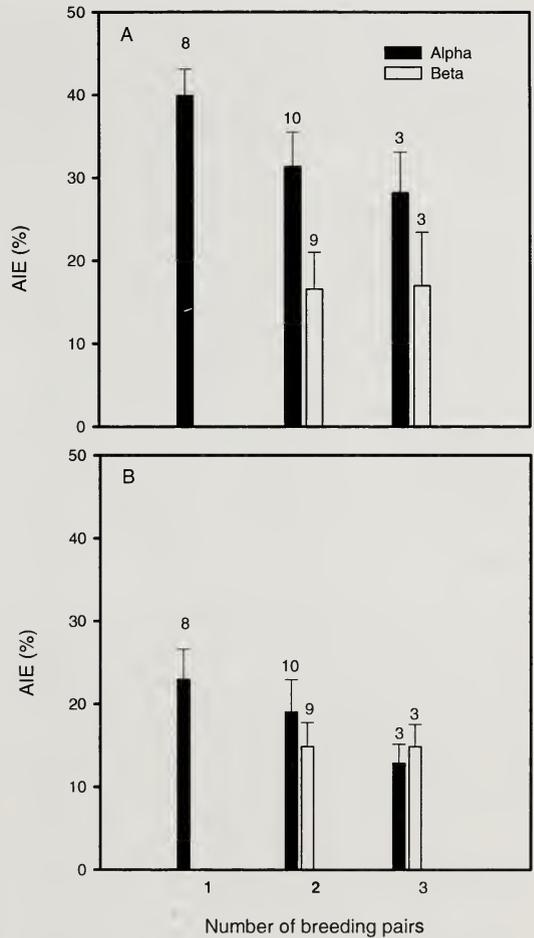


FIG. 3. Mean (± SE) absolute incubation effort (AIE) of (A) females and (B) males in different group sizes (number of breeding pairs) of Taiwan Yuhinas in Nantou County, central Taiwan, 2000–2001. Sample size (number of nests) shown above bars.

were no significant differences among other individuals in either RIE or AIE (Figs. 2 and 3).

*Incubation effort between sexes and group sizes of different status.*—Because there was a strong sex × status interaction, we further analyzed alpha and beta pairs separately. RIE of alpha females was greater than that of alpha males (GLM,  $F_{1,37} = 6.43$ ,  $P = 0.016$ ; Fig. 2) and RIE of the three group sizes differed (males and females combined, alpha birds only):  $46.25 \pm 2.58\%$  (one breeding pair),  $32.55 \pm 3.97\%$  (two breeding pairs), and  $22.52 \pm 4.32\%$  (three breeding pairs) ( $F_{1,37} = 16.24$ ,  $P < 0.001$ ; Fig. 2). There was no in-

teraction between sex and group size ( $F_{1,37} = 1.37$ ,  $P = 0.25$ ) or between the extra male and group size ( $F_{1,37} = 0.03$ ,  $P = 0.87$ ). AIE of alpha pairs differed marginally between the sexes (group sizes combined):  $20.22 \pm 2.44\%$  (males),  $34.16 \pm 2.54\%$  (females) ( $F_{1,37} = 3.78$ ,  $P = 0.059$ ; Fig. 3). AIE of alpha pairs also differed between group sizes (males and females combined, alpha birds only):  $31.44 \pm 3.20\%$  (one breeding pair),  $25.80 \pm 3.11\%$  (two breeding pairs), and  $20.53 \pm 4.19\%$  (three breeding pairs) ( $F_{1,37} = 4.04$ ,  $P = 0.043$ ; Fig. 3). Again, the interaction between sex and group size ( $F_{1,37} = 0.40$ ,  $P = 0.53$ ) and the interaction between the extra male and group size ( $F_{1,37} = 0.29$ ,  $P = 0.59$ ) were not significant. In beta pairs, all factors tested above did not significantly affect either RIE or AIE.

#### DISCUSSION

To our knowledge, this is the first study showing that constancy of incubation increases with increasing group size. Greater constancy of incubation may provide a more stable thermal environment, resulting in more rapid embryo development (Deeming 2002). This suggests that sharing the incubation effort does not necessarily lead only to "load lightening" of other breeders (Brown and Brown 1981, Crick 1992). Breeders may also maintain the same level of incubation effort, thus increasing overall incubation effort as more individuals participate. This response may be analogous to the "additive" effects of helpers during nestling provisioning (Hatchwell 1999), presumably increasing the fitness of breeders by increasing the number of offspring.

Here, we showed that both alpha males and females reduced their incubation effort when more individuals were present in the group. Beta pairs, however, maintained a constant effort when more individuals participated in incubation. This phenomenon explains why constancy of incubation varies positively with group size. Attracting additional group members reduces the cost of parental care for alpha individuals while providing improved incubation constancy. Given that the alpha females contribute more to incubation than other members of their respective groups, it is reasonable to expect that alpha females could

gain more benefit from larger groups in terms of lightening their work load. This may explain why the survival probabilities of alpha females, but not alpha males, increase with group size (Shen 2002).

In this study, alpha females contributed significantly more to diurnal incubation effort than other individuals. Yuan et al. (2004) found that female yuhinas also contribute more to nocturnal incubation. Female-biased asymmetry in parental care has long been attributed to a sex-bias in the uncertainty of parentage (Trivers 1972, Queller 1997). In cooperatively breeding species, it has been argued that selection favors male survival over parental care, whereas in females, selection favors behavior that promotes offspring survival, largely due to the fact that females have a greater confidence of parentage (Cockburn 1998, Hatchwell 1999). Extra-group paternity is high in yuhinas (21.4%; H-WY unpubl. data), and it seems appropriate to adopt the parentage uncertainty hypothesis to explain the high incubation effort of alpha females, but not males. However, in most joint-nesting species, the male does the bulk of incubating, especially at night (Vehrencamp 2000, Vehrencamp and Quinn 2004). A possible functional explanation for males taking over nocturnal incubation—which is energetically expensive and imposes a greater risk of predation—is that it allows their mates to produce larger clutches, lay replacement clutches, or contribute more to nestling care (Vehrencamp 2000). Moreover, the low incidence of extra-group paternity in those joint-nesting species may promote greater contributions of parental care among the males (review in Cockburn 1998); yuhinas, on the other hand, exhibit a greater extent of extra-pair paternity. Therefore, different fitness components must be considered to predict patterns of variation in parental investment strategies in complex social groups.

Although parental investment strategies developed according to provisioning effort can be analogous to incubation effort, as we have shown above, we believe that there are some important differences that need further examination. For example, are there any differences in parental investment strategies with respect to incubation effort and provisioning, and, if so, why? For cooperatively breeding mam-

mals, much more attention has been given to comparing division of labor of different activities, such as babysitting, pup feeding, and guarding, than for birds (Clutton-Brock et al. 2003). In birds, Magrath and Komdeur (2003) also argued that the tradeoffs between parental effort and mating effort have more commonly been observed during incubation than during the nestling feeding period in cooperatively breeding species, although little empirical evidence supports this view. Another related question is why there are fewer helpers in cooperatively breeding species participating in incubation. Clutton-Brock (1991) speculated that one stimulus for male help with incubation may be an attempt to minimize the probability that females will destroy each others' eggs. Few studies have been conducted to evaluate this hypothesis. Given that incubation is an important component of reproductive costs in birds (Reid et al. 2002a), it is surprising that there are so few studies dealing with parental investment strategies during incubation in cooperatively breeding birds.

Our study provides an example of different parental investment strategies exhibited by males and females during incubation, and a potential new group benefit of cooperative breeding that increases incubation effort. We also suggest that AIE should be a better measure than RIE of an individual's incubation effort. Because AIE reflects the real effort and cost of nesting that each individual contributes and bears, respectively, and because RIE represents only the relative contribution (potentially omitting additional information—as we found in this study), only AIE can indicate the extent to which work loads are lightened as group size increases. Future work on incubation in cooperatively breeding birds will give us a better understanding of the effect of helpers and co-breeders on other group members' parental effort and, thus, will have profound implications for the evolution of different investment strategies in different cooperative breeding systems.

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# Short Communications

Wilson Bulletin 117(3):313–315, 2005

## Rolling Prey and the Acquisition of Aerial Foraging Skills in Northern Mockingbirds

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**ABSTRACT.**—I describe an unusual food-handling behavior performed by juvenile Northern Mockingbirds (*Mimus polyglottos*). In the course of one morning, I observed juvenile Northern Mockingbirds repeatedly roll several prey items down the incline of a roof in Charlottesville, Virginia. I discuss this behavior in the context of the development of aerial foraging skills. Received 20 September 2004, accepted 26 April 2005.

Newly independent passerines are often inefficient foragers and are under selective pressure to acquire foraging skills quickly once parental care has ended (Weathers and Sullivan 1991). Foraging skills take time to master, and some types of foraging, such as aerial hawking, take longer to master than others (Moreno 1984, Marchetti and Price 1989). Object play, which often involves the dropping and catching of both food and non-food items, might be an important adaptive behavior that helps newly independent birds develop such foraging skills (Gamble and Cristol 2002). Instances of apparent solitary object play are occasionally reported in birds, but few such instances have been reported in non-corvid passerines (Ficken 1977, Diamond and Bond 2003). Here, I report an observation of unusual prey manipulation and possible object play in a non-corvid passerine, the Northern Mockingbird (*Mimus polyglottos*).

### OBSERVATION

On 27 July 2004, in suburban Charlottesville, Virginia, from 08:46 to 09:28 EDT (25° C, light rain), I observed a trio of juvenile Northern Mockingbirds on my neighbor's rooftop (~35° incline). I observed without binoculars for the first 10 min and with binoculars for the remaining time.

At 08:46, I saw three juvenile Northern

Mockingbirds perched on the peak of the roof. One of the juveniles (bird A) had an earthworm (4–5 cm in length, clitellum visible) in its beak. It dropped the worm, which formed into a ball and rolled down the roof about 1 m. Bird A ran after and grabbed the worm in its beak. The other two juveniles (B and C) pursued A. When B and C came within 0.5 m of A, A jumped up, flashed its white wing patches, and lifted its feet into the air (see Hayslette 2003 for more on wing-flashing). Birds B and C ran back up to the rooftop. Bird A then flew back to the rooftop, dropped the worm, let it roll 1 m down the incline, ran after it, grabbed the worm in its beak, thrashed the worm against the roof, dropped the worm, let it roll another 1 m down the incline, retrieved it and returned to the rooftop. Birds B and C ran toward A at the top of the roof, at which point bird A flew up about 1.5 m above the roof line, with the worm in its beak.

Two adult-plumaged Northern Mockingbirds flew onto the roof. One adult bird flew toward birds B and C, both of which flew off out of sight. Bird A jumped up and wing-flashed about 1 m from one of the adult Northern Mockingbirds. After a few minutes, the adult Northern Mockingbirds left. Bird A, now alone on the roof, spent the next 4 to 5 min rolling the worm down the roof, usually 1 m at a time, retrieving it, thrashing it on the surface of the roof, flying or walking back to the roof line, and rolling the worm down again. This behavior was repeated a total of seven times. Finally, bird A consumed the worm and flew out of sight at 08:56.

At 09:20, one juvenile Northern Mockingbird returned to the roof carrying a small winged insect (<2 cm in length) in its beak. It dropped the insect on the roof ridge, picked it up, and dropped it again, at which point the insect rolled about 0.3 m down the roof. The bird picked up the insect, ate it, and flew off.

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Five min later, one juvenile Northern Mockingbird returned with a large larva, 4–5 cm long, possibly *Ceratonia catalpae* (Wagner et al. 1997). The larva had roughly 10 parasitoid wasp pupae attached to its thorax. Two other juvenile Northern Mockingbirds arrived and harassed the owner of the larva. The owner dropped the larva, which rolled down the roof about 1 m. The owner retrieved the larva, brought it to the top of the roof, and thrashed the larva on the edge of the roof. This rolling, thrashing, and retrieving behavior was repeated three additional times. Some of the wasp pupae attached to the larva fell off during the thrashing. The owner then flew away with the intact larva in its beak. The two remaining juveniles alternately displaced each other and then flew off together. The birds did not reappear on the roof in the next 2 hr.

#### DISCUSSION

Newly independent Northern Mockingbirds in south Florida are less proficient at prey capture than adults (Breitwisch et al. 1987), and studies of Northern Mockingbirds and other passerines have revealed that proficient aerial foraging takes longer to achieve than proficient ground foraging (Moreno 1984, Breitwisch et al. 1987). The rolling of invertebrate prey, as reported here, is possibly a method that Northern Mockingbirds use to develop aerial foraging skills. Juvenile Northern Mockingbirds also have been observed picking up gravel and other inedible objects from the ground and then dropping them, possibly a result of inexperience with prey, but possibly an adaptive behavior involved in the acquisition of ground foraging skills (Breitwisch et al. 1987). In the present observation, the roof allowed the prey to roll away from the Northern Mockingbirds, but not as quickly as if dropped in mid-air. Therefore, the roof might provide a “safe” place for young birds to practice catching air-borne prey or retrieving prey dropped in mid-air (Gamble and Cristol 2002).

An alternate explanation is that the juvenile Northern Mockingbirds chose an inappropriate location to process prey items and the rolling was incidental. Many passerines, such as Spotted Antbirds (*Hylophylax naevoides*), thrash prey against hard surfaces prior to consumption (Willis 1972), and adult Northern

Mockingbirds in North Carolina have been observed to do the same (A. Skypala pers. comm.). The juveniles I observed simply could have chosen a poor place to thrash prey items.

This observation highlights the difficulty of determining whether instances of apparent play are an adaptive part of an animal's behavioral repertoire or whether they are incidental outcomes resulting from a lack of experience. Play is notoriously difficult to define and is frequently a catch-all term for any seemingly purposeless behavior, especially if it is observed in young animals (Martin and Caro 1985, Bekoff and Byers 1998, Diamond and Bond 2003). Distinguishing between adaptive play behavior and inexperience is challenging, but such distinctions can lead to insights about the selective pressures that shape learning (Martin and Caro 1985). Longitudinal studies following individuals would be required to determine whether Northern Mockingbirds that engage in prey rolling as juveniles are more efficient at aerial prey capture as adults or achieve aerial proficiency more quickly than birds that do not roll prey down inclines (Gamble and Cristol 2002).

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## Above-ground Nesting by Northern Bobwhite

Theron M. Terhune,<sup>1,3,4</sup> D. Clay Sisson,<sup>2</sup> and H. Lee Stribling<sup>1</sup>

**ABSTRACT.**—The Northern Bobwhite (*Colinus virginianus*) is one of the most studied game birds in North America. It is a ground-nesting galliform capable of producing multiple nests during a single season. Since 1993, personnel of the Albany Quail Project have radio-tagged >6,000 bobwhites and monitored >2,000 nests via radio telemetry on private lands in southwestern Georgia. We have observed nests in some peculiar places; however, every nest that we have monitored has been on the ground. Previously, no case of above-ground nesting has been documented for this species. Here, we report an above-ground nest, found in June 2001. *Received 27 September 2004, accepted 21 May 2005.*

Gallinaceous birds typically nest on the ground, and the Northern Bobwhite (*Colinus virginianus*) is no exception. Bobwhites usually nest in herbaceous vegetation consisting of mixed grasses and forbs, such as that found along fencerows and roadsides or in idle/fallow areas and other early successional habitats. The bobwhite has a propensity to nest near edges (usually within 15.5 m) of roads, fields, disked strips, or pathways (Stoddard

1931, Rosene 1969, Simpson 1972). Typical nests are constructed primarily of grasses (e.g., *Andropogon* spp.) and pine (*Pinus* spp.) needles, although other materials may include mosses, leaf litter, and tree-limb debris. It is well documented that bobwhites use a wide variety of nesting sites (Stoddard 1931, Rosene 1969, Simpson 1972, Klimstra and Roseberry 1975) and some are located in peculiar places (e.g., ditch banks, dense stands of hardwoods, and flowerbeds). Carter et al. (2002) reported the importance of prickly pear (*Opuntia* spp.) as nesting cover following a prescribed burn in Texas. Whereas bobwhite nesting ecology has been thoroughly studied throughout its range, above-ground nesting has not been reported in the peer-reviewed literature.

During the course of our ongoing studies for the Albany Quail Project, we have radio-tagged >6,000 bobwhites and found >2,000 nests. The study area is located on private lands in Baker County, southwestern Georgia (31° 21' 35" N, 84° 16' 18" W) in the Upper Coastal Plain physiographic region. Study sites are characterized by old-field pine forests with relatively low basal area that are intensively managed for bobwhite. Habitat management regimes typically include annual burning, seasonal disking, drum-chopping and mowing, supplemental feeding, and mammalian nest-predator control. As a result of these

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intense management regimes, these areas maintain abundant wild bobwhite populations ranging from 1.48 to 7.41 birds/ha (Yates et al. 1995; Sisson et al. 1997a, b).

Between 16 and 19 June 2001, an employee at one of our study areas watched a pair of bobwhites spend a considerable amount of time near a holly bush (*Ilex* sp.) in his front yard. We surmised that the female was nesting in the holly bush, and on 9 July, we returned to find 16 pipped bobwhite eggs in a nest in the bush. Several days later, we observed a brood near the holly bush. The nest was built above ground (76.2 cm), on top of a passerine nest (unknown species) composed of sticks and dead leaves. It was typical for bobwhite nests, however, having been lined with pine needles.

The above-ground nesting reported here may not be entirely novel among bobwhites, as Rosene (1969) reported a similar nesting record (a second-hand observation), from which 12 eggs hatched successfully. Above-ground nests have also been reported for other gallinaceous species, including Wild Turkey (*Meleagris gallopavo*) and Ring-necked Pheasant (*Phasianus colchicus*). Fletcher and Parker (1994) reported a Wild Turkey nest 2.4 m above ground in a live oak (*Quercus virginiana*). They speculated that the unusual nest site may have been selected to avoid depredation by raccoons (*Procyon lotor*) or feral hogs (*Sus scrofa*). Cobb et al. (1989) reported two separate instances in which Wild Turkeys nested above ground—on a log and on a stump in a water tupelo (*Nyssa aquatica*)/bald cypress (*Taxodium distichum*) swamp. Cobb et al. (1989) suggested that the anomalous nesting behavior was a result of the hens having experienced flooding of their nests during the preceding breeding season. Pheasants, especially tragopans (*Tragopan* spp.), also have been known to nest above ground (J. P. Carroll pers. comm.).

The aberrant nesting behavior we observed demonstrates the ability of bobwhite to use almost any available substrate. Of 2,117 nests that we found during the Albany study, 1,503 were in upland piney woods, 551 were in fallow fields, and 58 were in hardwood-domi-

nated sites; only 5 nests were in other habitats (ditch banks, creek swamps, cypress-pond edges, and flowerbeds). Whereas most (71%) nests were in upland piney woods, the remaining 29% were in areas lacking the bunch grasses more typical of bobwhite nesting habitat. Indeed, the range of nesting habitats reported indicates that bobwhites are much more opportunistic nesters than once realized.

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Divorce in the Canary Islands Stonechat (*Saxicola dacotiae*)Juan Carlos Illera<sup>1</sup>

**ABSTRACT.**—I report the first case of divorce for the Canary Islands Stonechat (*Saxicola dacotiae*), an endemic bird species of the semiarid island of Fuerteventura (Canary Islands, Spain). I studied 72 pairs during three breeding seasons (2000–2001, 2001–2002, and 2002–2003). In 2001–2002, a female divorced after a successful first nesting. This female settled in a neighboring territory where the owner was unpaired, built a new nest, and laid four eggs. The low rate of divorce (1.4%) suggests that unforced mate changes by Canary Islands Stonechats are rare. Received 22 July 2004, accepted 31 May 2005.

The Canary Islands Stonechat (*Saxicola dacotiae*) is an island endemic restricted to Fuerteventura Island, Canary Islands, Spain. Bibby and Hill (1987) estimated the population size of the species as 650–850 pairs. Although there are no recent estimates of the abundance of the species, its status has been modified recently by the Spanish Ornithological Society (SEO/BirdLife) from “Near Threatened” to “Endangered” on the basis of increasing destruction and alteration of its habitats (Illera 2004a). In spite of its critical status, very little is known about the biology of this species. Here, I describe the first case of divorce in the Canary Islands Stonechat.

The Canary Islands archipelago is located in the Atlantic Ocean, 100–460 km off the northwest coast of Africa, and comprises seven main volcanic islands and several islets. Fuerteventura is the easternmost (28° 46' N, 14° 31' W), second largest (1,660 km<sup>2</sup>), and oldest island (approximately 22 million years old; Carracedo and Day 2002). The climate is semiarid with dry summers and scarce rainfall in autumn and winter (mean annual precipitation = 117 mm; Marzol-Jaén 1984). The vegetation is mainly sparse xerophytic shrubland. Canary Islands Stonechats are largely re-

stricted to slopes of stony fields and ravines covered by medium to large shrubs and large boulders; they avoid lava and sandy habitats (Illera 2001). Stonechats are thought to be monogamous, sedentary, and territorial (Martín and Lorenzo 2001, Urquhart 2002, Illera 2004b). Territory boundaries usually abut those of neighboring pairs (JCI pers. obs.). After settling, individual birds are extremely faithful to their sites all year long, i.e., they do not move after the breeding season, although territory boundaries may shift between successive breeding seasons (Illera 2004b; JCI unpubl. data). The breeding period extends from December to April (Martín and Lorenzo 2001, Urquhart 2002, Illera 2004b; JCI unpubl. data). Reproductive effort and the duration of the breeding period depend proximately on rainfall and ultimately on food (arthropod) availability (Illera 2004b; JCI unpubl. data). Pairs breed over more extended periods and lay two clutches in wet years, whereas in dry years they breed only once or not at all. Clutches are also larger in wet than in dry years (Illera 2004b; JCI unpubl. data).

Results presented here were obtained during studies of stonechat breeding success and site fidelity. Birds were trapped, banded, and monitored (Illera 2004b; JCI unpubl. data). I monitored 72 pairs over three breeding seasons (2000–2001, 2001–2002, and 2002–2003) at 12 study sites in which 1–10 pairs bred at least once in the 3 years. Of 72 pairs, I color-banded 114 individuals: 32/42 (2000–2001), 39/47 (2001–2002), and 43/54 (2002–2003). Due to sexual dimorphism and individual variability in phenotypic traits, I was also able to identify unbanded individuals. However, because sexual dimorphism traits shift after the molt period (Illera and Atienza 2002), they were only used to identify individuals within each breeding season. The number of banded pairs studied during two or more breeding periods was seven. I monitored pairs at least weekly from late October to ear-

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ly November (pre-breeding period) until a month after the last fledgling left the nest (post-breeding period). The time spent monitoring each pair during each visit varied between 30 min and 2 hr. Stonechats nested once or not at all in the dry (27.3 mm rainfall) breeding season of 2000–2001, and laid two clutches in the two wet years (124.5 and 125.1 mm rainfall in 2002 and 2003, respectively; Illera 2004b; JCI unpubl. data).

Of 72 pairs monitored, only one divorced within a breeding season (2001–2002). Divorce was not recorded for pairs monitored ( $n = 7$ ) in successive breeding seasons. The case of divorce reported here was the result of desertion by a female that subsequently settled in a neighboring territory where the owner was unpaired. Desertion occurred after the original pair successfully reared a brood (three fledglings). In the first brood (about 15 days previous to divorce), during 90 min of observation, 9 and 10 feeding visits were performed by the female and the male, respectively. In six visits to this territory, I did not observe the second male assisting with feeding young or encounters between the female and the second male. All three adults were color-banded. Fifteen days after the first brood fledged, the female built a new nest and laid four eggs. Both members of the new pair fed nestlings of the second brood, with no assistance from the divorced male. The nest was depredated, but the new pair did not attempt to breed again, and 2 weeks later the female disappeared from the territory. The female's original mate continued singing and feeding its three chicks alone during the 4 weeks after fledging. The divorced female never returned to her former territory even though the territories were adjacent. The deserted male did not mate with another female during the remainder of the 2001–2002 breeding period, and he finally moved to a new territory 5 months later.

Limited information is available on divorce in the genus *Saxicola* (Urquhart 2002). Johnson (1961, 1971) recorded several cases of mate exchanges, polygyny, and polyandry in a population of Common Stonechat (*S. torquata*), both within a given breeding season and between successive breeding seasons. H. Flinks (*in* Urquhart 2002) reported that male Common Stonechats might be vulnerable to

mate loss while feeding fledglings. Bibby and Hill (1987) reported that some unpaired male Canary Islands Stonechats assist with feeding young of established pairs. However, during 238.5 hr of observation of feeding (23 pairs), I did not record males or females assisting with feeding young.

The low rate of within-season divorce (1.4%,  $n = 72$  pairs; three breeding seasons) and the lack of between-season divorce (0/7) suggests that unforced mate changes by Canary Islands Stonechats are rare. Strong site fidelity reported for this species (Illera 2004b; JCI unpubl. data.) also suggests that occurrences of between-season divorce are rare. Divorce did not appear to have been triggered by poor breeding success, as mean fecundity of all pairs monitored over 3 years was  $2.25 \pm 0.15$  SE ( $n = 68$ ). The biotic and abiotic homogeneity of Fuerteventura and the likely costs associated with territory switching (e.g., increased probability of predation after a move, aggression of adjacent territory holders, and less efficient foraging in unfamiliar territories; Jakob et al. 2001, Yoder et al. 2004) probably makes divorce maladaptive in this species.

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## Regurgitated Mistletoe Seeds in the Nest of the Yellow-crowned Tyrannulet (*Tyrannulus elatus*)

Peter A. Hosner<sup>1</sup>

**ABSTRACT.**—I describe a Yellow-crowned Tyrannulet (*Tyrannulus elatus*) nest built largely of mistletoe seeds, which differs from the cup of plant matter typically constructed by this species. Mistletoe seeds have been observed in the nests of at least two other bird species, but this observation is the first where the nest appeared to be purposely constructed from seeds, possibly to take advantage of their adhesive properties. Received 20 September 2004, accepted 31 May 2005.

Adhesive substances, such as the saliva of *Aerodramus* and *Collocalia* swiftlets (Smythies 1999, Hansell 2000), and regurgitated materials, such as fruits and seeds ingested by Oilbirds (*Steatornis caripensis*; Hilty and Brown 1986), are regularly used for nest construction by these and a few other bird species. However, the use of adhesive mistletoe fruit seeds in nest construction is almost unknown. There have been only two other reports of mistletoe seeds used in nest construction, both in nests of unrelated flycatcher spe-

cies (Tyrannidae: Traylor 1977; Lanyon 1984, 1988; Mobley 2002; Fitzpatrick 2004). A single atypical nest of Fork-tailed Flycatcher (*Tyrannus savana*) in Brazil contained mistletoe seeds regurgitated by an adult into the nest cup during incubation, apparently to help keep the loosely structured nest from falling apart (Sick 1985). Other descriptions of *T. savana* nests make no mention of mistletoe seeds (Hilty and Brown 1986, Stiles and Skutch 1989, Howell and Webb 1995, Hilty 2003, Fitzpatrick 2004). In Venezuela, a single globular nest of the Great Kiskadee (*Pitangus sulphuratus*) was observed to contain a few regurgitated mistletoe seeds about the lower rim and below the side entrance to the nest (J. A. Mobley pers. obs.). No published descriptions of *P. sulphuratus* nests mention mistletoe seeds (Hilty and Brown 1986, Stiles and Skutch 1989, Howell and Webb 1995, Hilty 2003, Fitzpatrick 2004). Here, I provide the first report of a nest covered almost entirely with mistletoe seeds, by the Yellow-crowned Tyrannulet (*Tyrannulus elatus*).

Birds, including *T. elatus* (Hilty and Brown

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1986, Stiles and Skutch 1989, Hilty 2003, Fitzpatrick 2004), are well-known consumers and dispersers of mistletoes (Viscaceae, Loranthaceae) in the Neotropics (e.g., Calder and Bernhardt 1983, Sargent 1994, Restrepo et al. 2002). However, other uses of these plants by birds are poorly known. The seeds of some mistletoe species contain an extremely adhesive layer of viscin tissue under the fruit flesh; once digested, viscin can sometimes elongate to form a thread 3–4 cm long that is attached to one end of the seed. During regurgitation or defecation of the seed, the loose end of this thread will stay in the stomach or cloaca until it is wiped on a substrate, usually a branch. Leverage is then used to remove the strand entirely from the body (Kuijt 1969, Calder and Bernhardt 1983). This is an effective dispersal strategy for mistletoes, as the seeds are occasionally placed on a branch in a location suitable for germination.

The *T. elatus* nest was found on 20 March 2004, on Barro Colorado Island, Panama (9° 9' 49" N, 79° 50' 16" W; 80 m in elevation) in a clearing in humid, lowland evergreen forest. When found, the nest was complete and contained a single egg. The nest was placed approximately 7 m above ground on a small horizontal branch—about 2 cm in diameter—in a 20-m broadleaf evergreen tree parasitized by several mistletoe plants, on which the flycatcher pair fed. The cup-shaped nest was small, approximately 5 cm in diameter (outside rim to outside rim), and was built of undetermined plant material. Regurgitated seeds covered the entire exterior of the nest, and there was a band of regurgitated seeds that wrapped beneath the branch on which the nest was built. Seeds were also worked into the plant material in the nest's interior.

The mistletoe seeds were probably of the genus *Struthanthus* or *Oryctanthus*, with *Struthanthus* more likely based on the round (as opposed to more ovoid) seed shape (S. Sargent pers. comm.) Upon regurgitation, the seeds were a whitish color, but seeds already placed on the nest had dried and turned a crimson-red to orange-red color. The single egg was white with small, evenly dispersed blotches of pale cinnamon to raw umber. The color appeared to be from pigment in the eggshell rather than from stains from the mistletoe seeds, as the colors were different. The

nest did not appear large enough to accommodate a second egg. Nest-construction materials and the pattern of egg markings differed from those described in other published accounts (Penard and Penard 1910, Snethlage 1935, Hilty and Brown 1986, Stiles and Skutch 1989, Hilty 2003, Fitzpatrick 2004); these authors described the nest as a shallow cup built of small twigs, mosses, spiderwebs, grasses, tree bark, feathers, and other fine material, and containing a clutch of two unmarked white or cream-colored eggs. A nest of *T. elatus* found in the same clearing on Barro Colorado in 2003 (R. Moore pers. obs.) was similar to the published descriptions; therefore, the nest built of mistletoe seeds was not likely to have been a local adaptation.

On 20 March 2004, the bird attending the egg (distinguishable from its mate by awkwardly arranged feathers on the crown) left for short foraging bouts that lasted ~5 min. Upon returning to the nest, it would resume incubation, and then regurgitate three to four additional seeds on the nest. The bird then used its bill to move the seeds to a location on the nest's exterior, or work them into the plant material in the cup wall, thus continuing to construct the nest after the egg was laid. Placement of each seed took a short period of time—between 5 and 15 sec in 3 hr of observation. I observed four such foraging bouts followed by seed regurgitation and placement. Both the attending bird and its mate also wiped regurgitated seeds on branches in the nest tree. Both adults actively defended the territory against Palm Tanagers (*Thraupis palmarum*) and Social Flycatchers (*Myiozetetes similis*), two other species that may consume mistletoe fruits.

Two hypotheses might explain wiping mistletoe seeds on nests: either the adhesive properties of the seeds were used intentionally to aid in nest construction, or the nest was simply the most convenient object on which the incubating bird could wipe seeds. The careful placement of regurgitated seeds by *T. elatus* on the nest exterior, however, suggests that the seeds were being intentionally used for their adhesive properties to hold the small nest together and to adhere it to the branch. Placing seeds underneath the supporting branch and working seeds into the nest cup takes more concentrated effort and care compared to wip-

ing them on the side of the nest or a nearby branch. Because mistletoe seeds are adhesive and viscin strands are strong, it seems possible that the seeds were used to strengthen the nest, perhaps allowing the overall size of the nest to be smaller than previously described nests, which would decrease the effort needed to build a nest. Because the bright, red-orange color of the seeds contrasted strongly with the surroundings, it seems unlikely that the seeds were used as camouflage.

Conversely, Sick's (1985) description of the *T. savana* nest and J. A. Mobley's (pers. comm.) observations of *P. sulphuratus* nests indicate that the addition of mistletoe seeds to the nest may be only a convenient means of wiping seeds while incubating, with no intent to alter nest structure. Sick (1985) suggested the seeds were inadvertently voided in the nest; neither he nor J. A. Mobley (pers. comm.) observed active placement of, or nest building with, mistletoe seeds, and the few seeds present were not enough to affect nest construction.

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# Ornithological Literature

Edited by Mary Gustafson

**BIRDS OF CHILE.** By Alvaro Jaramillo, illustrated by Peter Burke and David Beadle. Princeton University Press, Princeton, New Jersey. 2003. 240 pp., 96 color plates. ISBN: 0691004994, \$55 (cloth). ISBN: 069117403, \$29.95 (paper).—South America has the most extensive bird fauna of any continent, yet for many years lacked adequate field identification guides. For much of the continent, the lack of field guides has now been remedied with a series of books that vary in quality; however, for temperate South America, there were no good (and readily available) field guides. Now, with the present work, one more piece of the jigsaw puzzle has been provided—extremely well.

The book sets out to be a field identification guide, so does not purport to provide information on such topics as nesting or ecology that might be expected in a more comprehensive type of handbook. It employs the user-friendly “facing-page” format; that is, the illustrations are on one page and the text and range-maps are on the facing page, saving the inconvenience of having to look in two places at once. The text and plates make up the bulk of the book’s 192 pages. There is a useful one-page introduction; four pages on how to use the book; three informative pages on Chilean habitats; worthwhile sections on migration, vagrancy, seabirds, field identification, and conservation; and a glossary. At the rear of the book is an excellent appendix on current taxonomic problems—which are numerous—and I am glad to note that the author is not afraid to admit that more work is needed to resolve these taxonomic issues.

In the field-identification section, there is a brief general comment at the top of the page on the species or genera therein. Each species account includes a comprehensive section on identification and how to distinguish the species from similar-looking species, and notes about habitat, calls, and songs. The plates illustrate the most important features of each species; sexes and immature plumages are illustrated where necessary, as well as some

distinctive races. Occasionally, little vignettes are included, illustrating such things as the feeding behavior of storm-petrels or close-ups of the bills of flamingoes. The book also provides one of the best treatments that I have read on molt sequences in gulls, terns, and jaegers and how they affect identification; this information could be just as useful in North America as in Chile.

Above all else, a field guide will be judged by the quality of its plates, and the plates in *Birds of Chile* are excellent. Having more than one artist contribute to a field guide often leads to an unsatisfactory final product, given differences in the styles and abilities of the artists; that is not the case here. Burke and Beadle have compatible styles, and the overall standard of the illustrations is very high.

The format and size of the book limit the scope of the species accounts; nevertheless, all relevant details necessary for identification are given, and the book was obviously written by a field ornithologist for field ornithologists. Emphasis is given to truly useful field identification features rather than details more appropriate for a museum collection. The combination of text and plates is superior to that of any other book presently and easily available for the same geographic area. In addition to Chile, the book also covers the Falkland Islands, South Georgia, and the area of Chilean claims in Antarctica (which overlap with Argentinean and British claims—including the South Shetlands, the South Orkneys, and the Antarctic Peninsula).

For other field guides, I have frequently been critical of the range maps, which often seem to be ill-considered afterthoughts with little regard for clarity or accuracy. This does not apply here. Admittedly, Chile—which is as narrow as 100 km in some places but has a latitudinal span equal to that between Washington, D.C., and the mouth of the Amazon—presents a unique mapping problem that has been solved by splitting the maps into as many as three sections. This takes a little get-

ting used to, but the maps convey the species' ranges legibly and precisely.

One rather pleasant feature of the book is the inclusion of local Spanish (or rather, Chilean) names for birds. This feature will be useful in talking to locals, who are frequently knowledgeable about local fauna but unfamiliar with official names—just as a Newfoundland fisherman will look at you blankly when asked about Long-tailed Ducks (*Clangula hyemalis*) or Greater Shearwaters (*Puffinus gravis*), but will tell you exactly where to find the “hounds” and the “hagdowners.” In fact, some of these local names are much more picturesque and poetic than the clumsy English-language equivalents. For example, the Wren-like Rushbird (*Phleocryptes melanops*) is a “worker,” the White-tailed Kite (*Elanus leucurus*) a “dancer,” the Groove-billed Ani (*Crotophaga sulcirostris*) (mysteriously) a “horse-killer,” and nightjars are “blind hens.” With names like these, who needs polysyllabic and humorless official versions anyway?

The book contains a few errors, the most blatant being much missing text (at least in my copy) in the account on the Juan Fernandez Firecrown (*Sephanoides fernandensis*), undoubtedly due to someone inadvertently pressing the delete key. A determined nitpicker could list a few more errors; however, the function of a reviewer is to give an overall appraisal of the success or failure of a work rather than to zero in on trivia (the missing text on the firecrown can be obtained at [www.birdsofchile.com/errata.htm](http://www.birdsofchile.com/errata.htm)), and I find that the *Birds of Chile* is an excellent addition to the literature on South American birds. Not only will it be essential to anyone visiting this “skinny little country” (to quote the author), it will also be extremely useful to visitors of nearby countries for which there are no good field guides—notably Argentina and, to a lesser extent, Bolivia. With this in mind, the present work would have proven more useful if it had provided the non-Chilean ranges of species. This could have been done in a concise and abbreviated format without adding significantly to the length of the text. Apart from this minor quibble, the author, artists, and publishers have produced a field guide of superior quality and reasonable price. They are to be commended for a job well done.—DAVID

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**PENGUINS: LIVING IN TWO WORLDS.**  
By Lloyd S. Davis and Martin Renner, illustrated by Sarah Wroot. Yale University Press, New Haven, Connecticut, 2004: 200 pp. + xii, 8 color plates, 28 line drawings, 20 black and white photos, 27 graphs, 7 tables. ISBN: 0300102771. \$40 (cloth).—One of two major themes in this book is that penguins must be like fish because they spend most of their lives at sea; but because they are birds and therefore lay eggs, they must also have attributes that allow a terrestrial existence while breeding. Throughout the text, then, the authors describe the specializations and compromises involved in this bimodal lifestyle. Such is the lifestyle of all seabirds to greater or lesser degrees, but the penguins have exploited the aqueous environment like no other group of extant avian species, with the exception of loons and grebes. However, as the authors point out in a chapter on evolution, the penguins stand alone in their adaptations to swimming and diving among the several families that are flightless.

The book's other major theme revolves around the dichotomy in natural history patterns that exists between inshore and offshore foragers. I have always been annoyed at the use of such terms in the literature on seabirds or other marine taxa because these terms lack substance and are confusing in this context. For example, I have seen them used in habitat descriptions of Antarctic krill (*Euphausia superba*). What Davis and Renner really mean is that some species of penguins forage close to penguin colonies and others forage farther away—the cutoff for their purposes being 50 km. The terms inshore and offshore connote habitat rather than distance. If authors mean distance traveled during foraging—and I just reviewed a paper that used 40 km to distinguish inshore from offshore locations—then they should say so (i.e., short- versus long-distance foragers). If they want to connote foraging habitat, then the appropriate terminology would be neritic versus pelagic, with the continental slope being a transitional habitat that lies between them. Treating this terminology with more rigor has become even more

critical these days as, following the lead of Henri Weimerskirch and others, more and more researchers are evaluating the distance and duration of foraging trips to determine whether parents are foraging more for themselves or more for their offspring relative to their own energetic state or condition.

The inshore versus offshore dichotomy elaborates on the theme that Davis, along with J. P. Croxall, had emphasized in a summary paper presented at the Third International Symposium on Penguin Biology (Croxall and Davis. 1999. Penguins: paradoxes and patterns. *Marine Ornithology* 27:1–12). In the present volume, the authors cite Croxall and Davis' paper several dozen, and perhaps as many as 100, times. I definitely agree with their line of thought—that there is a distinct divergence in the natural history patterns of penguin species that are sedentary and forage close to the colony year-round versus species that are seasonally migratory and travel long distances to forage during breeding (Ainley et al. 1983. *Breeding Biology of the Adélie Penguin*. University of California Press, Berkeley).

The present volume certainly presents the topics a reader might expect from a book about penguins. *Penguin Evolution* (taxonomic placement depending on method of analysis); *Penguins Today* (thumbnail sketches of the existing species); *Living in Two Worlds* (mostly examples of the different life-history patterns of short- versus long-distance foragers); *A Place to Breed* (nest selection and habitat); *Mate Selection and Courtship*; *Parental Investment* (includes physiology of breeding, mate coordination); *Moult and Migration*; and *Conservation* (the majority of the world's penguin species are in jeopardy). What the reader will find, however, is not a review of the vast penguin literature; rather it is a thorough review and integration of Lloyd Davis' past 25 years of research and that of his students—Martin Remmer (the second author) being one of them. This is great, as Davis' research—mainly on behavioral and physiological aspects of penguin natural history (his forte, mostly to be found in chapters 6 and 7)—has been marvelously creative, and he has inspired his students to be likewise. Many of his students' theses have remained unpublished, which is not unusual, but, combined with his

own research, their body of work has greatly advanced our understanding of penguin biology. With this book, we have it all integrated in one volume. Moreover, this is not just a review; the text advances new ideas as well. Of course, the content of books almost never reaches electronic databases, which means that one downside to Davis and Renner's approach is that some of the ideas in their book may languish for a long time before being rediscovered by particularly erudite students of penguin biology.

One warning to prospective readers: although the writing is somewhat "folksy" in places, the fact that the authors present new ideas and interpretations—as well as the argumentative nature of some of their points (they take exception to how others have interpreted certain issues)—means that this book is not a quick read. Rather, be prepared to take the time to consider their points versus what has been said elsewhere in the penguin literature. For people who are serious about scratching below the surface of information on penguin biology, I definitely recommend this book.—DAVID AINLEY, HT Harvey and Associates, San Jose, California; e-mail: [dainley@penguinscience.com](mailto:dainley@penguinscience.com)

LOOKING FOR MR. GILBERT: THE RE-IMAGINED LIFE OF AN AFRICAN AMERICAN. By John H. Mitchell. Shoemaker & Hoard, Washington, D.C. 2005: 280 pp., 16 black-and-white photographs. ISBN: 1593760264. \$26 (cloth).—At first glance, this book does not seem a likely candidate for review in an ornithological journal, but the story has links to ornithology that those with an interest in the history of ornithology should find noteworthy. The book relates the historical sleuthing of the author in an attempt to recreate the life of an African American, Robert Alexander Gilbert, who lived from 1869 to 1942. For 24 years, Gilbert was the manservant and field companion of William Brewster, a major figure in the founding of the Nuttall Ornithological Club and the American Ornithologists' Union. The author discovered about 2,000 photographic glass plate negatives (mostly of New England scenery) in the attic of the offices of the Massachusetts Au-

dubon Society that were attributed to William Brewster, the society's first president. The author came to believe that these photographs, taken between 1888 and 1917, were mostly the work of Brewster's servant, Robert Gilbert. Intrigued by his findings, the author searched archives and interviewed people from the Museum of Comparative Zoology (MCZ) at Harvard University, and even traveled to Paris, France, in an attempt to rediscover and reconstruct the life of Gilbert.

Born in Virginia, Gilbert had moved to Boston and, at age 27, was hired by Brewster—a wealthy Boston Brahmin whose passion was ornithology—to help him set up his private museum in Cambridge. Gilbert was very bright and learned ornithology quickly; he became Brewster's chauffeur, mechanic, photographer, bird spotter, bird skinner, and general ornithological aid for the next 24 years until Brewster's death in 1919. Brewster bequeathed his large collection of bird skins to the MCZ, and Gilbert became an assistant curator there, a job he held off and on for the remainder of his life. He became the chef for MCZ Director Thomas Barbour's famous "Eateria," a daily luncheon at the museum, visited by notables and featuring such exotic fare as elephant's-foot stew.

Gilbert accompanied Brewster on his peregrinations from October Farm on the Concord River to Lake Umbagog in Maine and, on several occasions, to Europe. In later years, Gilbert contributed bird records and observations of behavior to Brewster that were eventually incorporated in Brewster's four-volume set *Birds of the Lake Umbagog Region of Maine*. While reading the extensive Brewster journals and other archival materials, the author unearthed some fascinating bits about Louis and Alexander Agassiz, Thomas Barbour, and Barbour's predecessor at the MCZ, Samuel Henshaw, and he quotes conversations with notables, including one with Ernst Mayr.

Most of the book deals with facets of Gilbert's life that were non-ornithological, including the racism encountered by African Americans in the late 19th and early 20th centuries. The author paints a convincing picture of life in a bygone era, providing biographical information on the life and times of William Brewster. The book is beautifully written and poignant. The book is not without errors, how-

ever: Richard Paynter at the MCZ should be Raymond A. Payntor, Jr., and the Nuttall Club did not change the name of its *Bulletin* to *The Auk*—that occurred after the Nuttall Club had handed over the subscriber list to the fledgling American Ornithologists' Union. This book is an interesting read, and although it is without references—and, as the subtitle "Reimagined Life" suggests, incorporates a great deal of supposition—it is nevertheless an interesting contribution to the history of American ornithology.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

HUMMINGBIRDS OF NORTH AMERICA. By Sheri Williamson and John W. Vanderpoel. Peregrine Video Productions, Niwot, Colorado. 2004: 178 minutes. VHS \$34.95, DVD \$39.95.—This video is the third in the Advanced Birding Series by Peregrine Video Productions, following the two videos on gull identification. The format will be familiar to those who have seen the gull videos, with Jon Dunn providing the narration and acting as a personal guide throughout the video. I particularly enjoyed Jon's asides on such subjects as how the vocalizations of an Anna's Hummingbird (*Calypte anna*) sound like a "familiar" typewriter to him—before he acknowledges that the typewriter is not as familiar as it once was. The identification information is commensurate with that presented in the gull videos, although the editing and overall presentation of the information is perhaps more polished.

The video begins with introductory material on watching hummingbirds, identifying hummingbirds, and documenting rarities. Those who want a pretty video with lots of exquisite footage of hummingbirds will be only partially satisfied with this tape. While the video is generally of extremely high quality, the focus is not on a celebration of these feathered jewels, but on the skills and knowledge needed to enable the observer to identify them in the field, which leads to technical discussions of feather shapes, primary width, and the like. The video is shipped with an insert that shows the topography of a hummingbird and defines some general terms. The insert also lists the

starting time for each species covered, enabling the viewer to select species of interest quickly. The film is also available on a DVD.

Twenty-four species are covered in depth, with a brief mention of two additional species—Amethyst-throated (*Lampornis amethystinus*) and Azure-crowned hummingbird (*Amazilia cyanocephala*)—that have not been documented in the U.S. or Canada. All breeding species of the U.S. and Canada are included. It is important to note that, although this video is titled *Hummingbirds of North America*, Mexico is not included. Non-breeding species include the Bumblebee Hummingbird (*Atthis heloisa*), Bahama Woodstar (*Calliphlox evelynae*), Cuban Emerald (*Chlorostilbon ricordii*), Xantus's (*Hylocharis xantusii*) and Cinnamon hummingbirds (*Amazilia rutila*), Green Violet-ear (*Colibri thalassinus*), Green-breasted Mango (*Anthracothorax prevostii*), and Plain-capped Starthroat (*Helio-master constantii*). The video categorizes hummingbirds into four large groups by general coloration (Rufous-Green and Gray-Green groups) or body size (Small Tropical and Large Hummingbird groups). The Rufous-Green and Gray-Green groups are further subdivided, thus leading viewers to the genus level—so necessary in hummingbird identification, particularly for birds in female and immature plumages.

The video's approach is straightforward, with a brief discussion of relevant characteristics for a given group or genus followed by detailed discussions of each species in the group. The species discussions include visual presentations of measurements, including weight, bill, and tail length. An animated map of each species' geographical distribution and breeding and wintering ranges is presented, and extralimital records are mapped. For species breeding in the U.S. and Canada, the courtship-display dive is illustrated and the

nesting chronology is described. This is followed by an overview of similar species and a discussion of vocalizations—including a sonogram of the calls—created by the Cornell Laboratory of Ornithology's Raven software. The structure or "jizz" of each species is reviewed, and then the plumage and characteristics of each age/sex class are discussed in some detail and compared with similar species or other age/sex classes, as needed.

The quality of the footage of hummingbirds is nearly uniformly excellent. Some footage was selected that has distant or backlit birds to emphasize points about size or shape, but the identification footage is generally of high quality, with sharp, well-lit birds. Nearly all the footage is of wild hummingbirds; an exception is video from the aviary at the Arizona Sonoran Desert Museum, used to illustrate, in particular, a female Lucifer Hummingbird (*Calothorax lucifer*). To me, it is preferable to use film of captive individuals if high quality footage of wild birds is not available.

This video is highly recommended to anyone with an interest in learning more about hummingbird identification. It is not labeled as a beginner's guide; however, birders using modern field guides and with an interest in learning more will find it a useful tool, although the depth of information presented may be intimidating initially. For advanced birders—the target audience for the series—this video will enhance their hummingbird identification skills and enjoyment when observing hummingbirds. Ornithologists will find that the information on field identification of hummingbirds, including the details on age/sex classes, will increase the reliability of their identifications in the field. Banders will find tidbits to use as well; I know I did!—MARY GUSTAFSON, Patuxent Wildlife Research Center, Laurel Maryland; e-mail: MGustafson@usgs.gov





## THE WILSON BULLETIN

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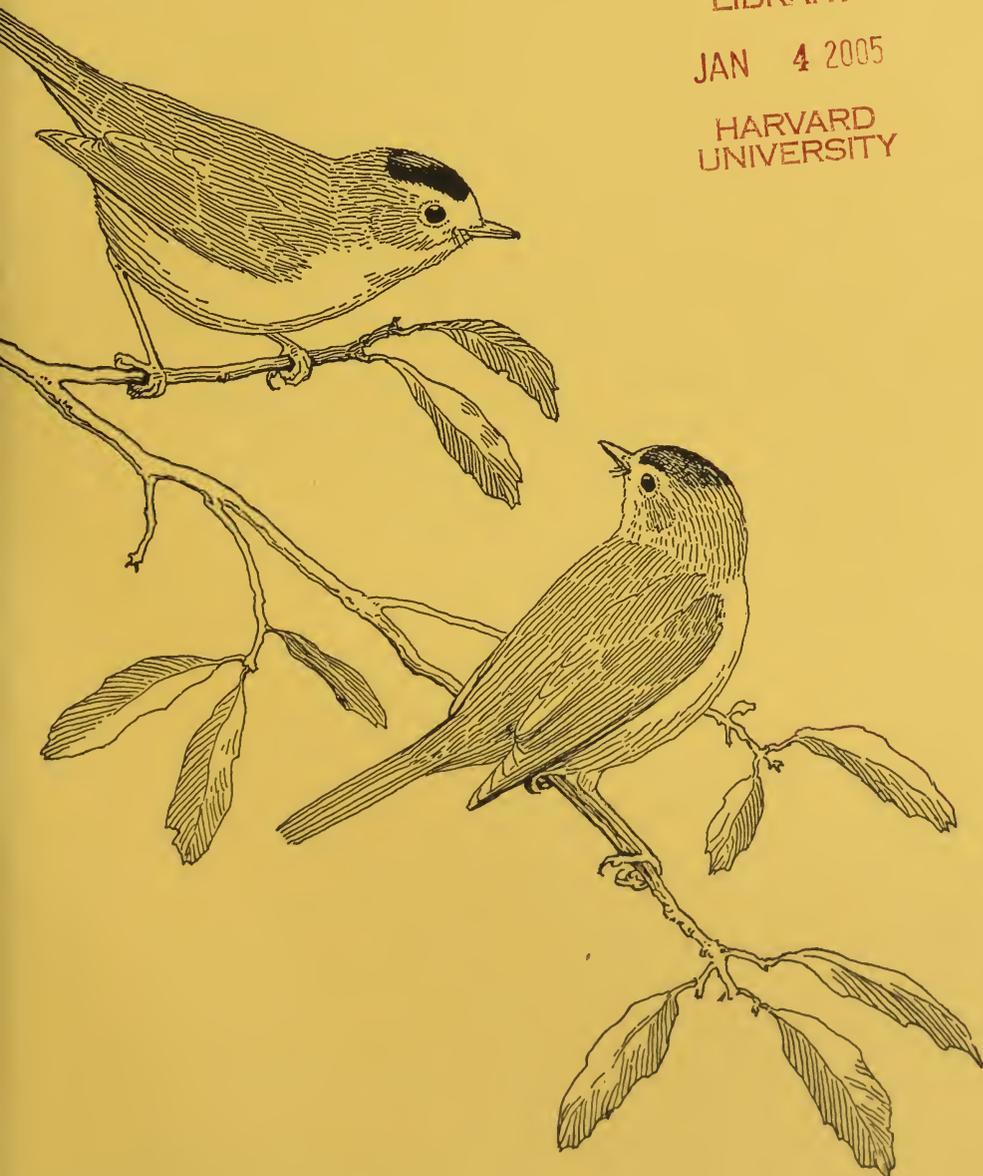
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FRONTISPIECE. Ovenbirds (*Seiurus aurocapilla*) at the Hemlock Hill Biological Research Area in Pennsylvania avoid forest interior and occupy only regenerating forest edges. Eastern chipmunks (*Tamias striatus*), abundant in forest interior but nearly absent in Ovenbird territories at Hemlock Hill, appear to influence this atypical habitat selection—highlighting the importance of general, simple cues to habitat selection. Original painting (watercolor) by Don Radovich.

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## PREDATION AND VARIATION IN BREEDING HABITAT USE IN THE OVENBIRD, WITH SPECIAL REFERENCE TO BREEDING HABITAT SELECTION IN NORTHWESTERN PENNSYLVANIA

EUGENE S. MORTON<sup>1,2</sup>

**ABSTRACT.**—From 1971 through 2003, Ovenbirds (*Seiurus aurocapilla*) at the Hemlock Hill Biological Research Area in northwestern Pennsylvania never bred in forest interior. Instead, they exhibited atypical habitat selection for breeding by occupying regenerating forest edges. Pairs in 14 territories, the entire population, showed normal annual return rates and pairing rates compared with other studies. For this ground-foraging bird, other studies showed that deep soil litter is preferred—but at my study site, soil litter depth in Ovenbird-occupied areas was lower than that found in the unoccupied forest interior. During May, July, and August, songs played in forest interior to attract Ovenbirds to settle there were unsuccessful. I tested the hypothesis that eastern chipmunk (*Tamias striatus*) abundance influenced this atypical habitat selection. Chipmunks were nearly absent from Ovenbird territories, but were abundant in the forest interior. I discuss habitat selection in birds in relation to simple cues and relate this to variation in habitat selection and use found in Ovenbirds. *Received 29 December 2004, accepted 9 August 2005.*

The Ovenbird (*Seiurus aurocapilla*) is a classic example of a “forest interior” and “area sensitive” songbird (Frost 1916, Forman et al. 1976, Ambuel and Temple 1983, Kroodsmma 1984, Gibbs and Faaborg 1990, Freemark and Collins 1992). In some areas, it avoids edge habitat altogether, irrespective of forest patch size (e.g., Missouri; Van Horn et al. 1995), but in other areas it does not appear to do so (e.g., New Brunswick [Sabine et al. 1996], Saskatchewan [Mazerolle and Hobson 2003]). In areas where Ovenbirds do breed in both edge and forest interior, edge-inhabiting birds often do poorly, suggesting that they are forced from preferred habitat and are making the best of a bad situation. However, they do not always have poor success in edge (Table 1). That Ovenbirds

may sometimes avoid forest interior and use only edge for breeding has not been previously reported.

A species with a wide breeding distribution might show geographic differences in habitat preferences, because habitat selection and use by breeding birds is based upon a complex mix of ultimate and proximate forces (Lack 1971, Cody 1985, Hutto 1985, Jones 2001). The costs and benefits of using available habitats may be influenced by predation, nest site, or food (Hutto 1985). In addition, intraspecific competition may force birds into marginal habitat (Fretwell and Lucas 1970), obscuring relationships between habitat preference, quality, and use. One would expect habitat use to vary if costs and benefits change geographically, even if the cues individuals use in selecting habitat are simple (e.g., a single element, such as light intensity, out of the multitude of features found in complex natural habitats).

Cues to habitat selection must be simple if

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TABLE 1. Regional variation in reproductive and pairing success of Ovenbirds in edge habitats versus forest interior in North America.

Location	Reproductive success <sup>a</sup>	Pairing success <sup>a</sup>	Reference
Northern Missouri	Lower	Lower	Van Horn et al. 1995
Central Missouri	? <sup>b</sup>	No difference <sup>c</sup>	Porneluzi and Faaborg 1999
Southern Indiana	No difference	?	Ford et al. 2001
New Jersey	?	Lower	Wander 1985
Northern Wisconsin	No difference	No difference	Flaspohler et al. 2001
North-central Minnesota	Lower	?	Manolis et al. 2002
Alberta	No difference	No difference	Lambert and Hannon 2000
Southern Saskatchewan	?	Lower	Bayne and Hobson 2001
Southern Saskatchewan	?	No difference	Mazerolle and Hobson 2003
Northern New Hampshire	No difference	No difference	King et al. 1996
Southern Ontario	Lower	Lower	Burke and Nol 1998
Quebec/Ontario	?	No difference	Villard et al. 1993

<sup>a</sup> Along forest edge (0–100 m) as compared with interior.

<sup>b</sup> No data.

<sup>c</sup>  $P > 0.05$ , or as stated by authors.

they are genetically grounded (Lack 1971, Partridge 1978). Laboratory studies of habitat-choice cues by naive birds have supported the ideas of both genetic basis and cue simplicity (Partridge 1974). Morton (1990) showed that nonbreeding female Hooded Warblers (*Wilsonia citrina*) chose habitats with oblique trunks and branches, whereas males chose habitats with vertical structures, irrespective of vegetation height. Breeding habitat consists of a mix of these oblique and vertical habitat features (James 1971). Greenberg (1992) showed that both Swamp (*Melospiza georgiana*) and Song sparrows (*M. melodia*) choose habitat differing in a single cue, the presence of water, and that this cue was innate. Innate cues are one element in predicting settlement patterns and these are probably due to selection over ultimate time scales. Proximate cues are more likely to involve individual assessment of costs. Predators, for example, can make otherwise suitable habitat unusable (Block and Brennan 1993). General habitat-selection cues may coexist with microhabitat cues, such as those important in avoiding nest predation (Martin 1998). These factors have not been well studied.

Here, I report a study of habitat use by Ovenbirds in northwestern Pennsylvania, where they use only edge habitat contiguous to mature, deciduous forest-interior habitat. I show that this aberrant selection of breeding habitat appears to be influenced by predators, notably the eastern chipmunk (*Tamias striatus*). I also

describe a playback experiment designed to attract Ovenbirds to settle in forest-interior habitat. My results, and those of others, show that habitat usage may vary across diverse geographic areas.

## METHODS

*Study area.*—The study took place at the 150-ha Hemlock Hill Biological Research Area (HHBRA), Crawford County, in northwestern Pennsylvania (41° 46' N, 79° 56' W), which is characterized by mature beech (*Fagus* spp.), maple (*Acer* spp.), oak (*Quercus* spp.), hickory (*Carya* spp.), and hemlock (*Tsuga* spp.) forest (Fig. 1; see also Howlett and Stutchbury 1996). Elevations range from 305 to 396 m and the terrain is largely flat or gently sloping. HHBRA is situated in an area fragmented by agriculture. Total forest cover for the region (740 km<sup>2</sup>) was 39% (Fraser and Stutchbury 2004) and 63% within a radius of 2 km of HHBRA (Rush 2004). HHBRA is surrounded by roads, fallow and active agricultural fields, and second-growth forest from 20 to 45 years old. To facilitate the mapping of territories, the entire 150-ha research area was grid-marked at 50-m intervals with orange plastic stakes in the ground and yellow flagging on trees. Beginning in 1971, and annually thereafter, I censused the entire area for breeding Ovenbirds. Censuses were conducted from 1 May to 1 July by listening for singing males, often in conjunction with ongoing studies of other species (e.g., Stutchbury et al.

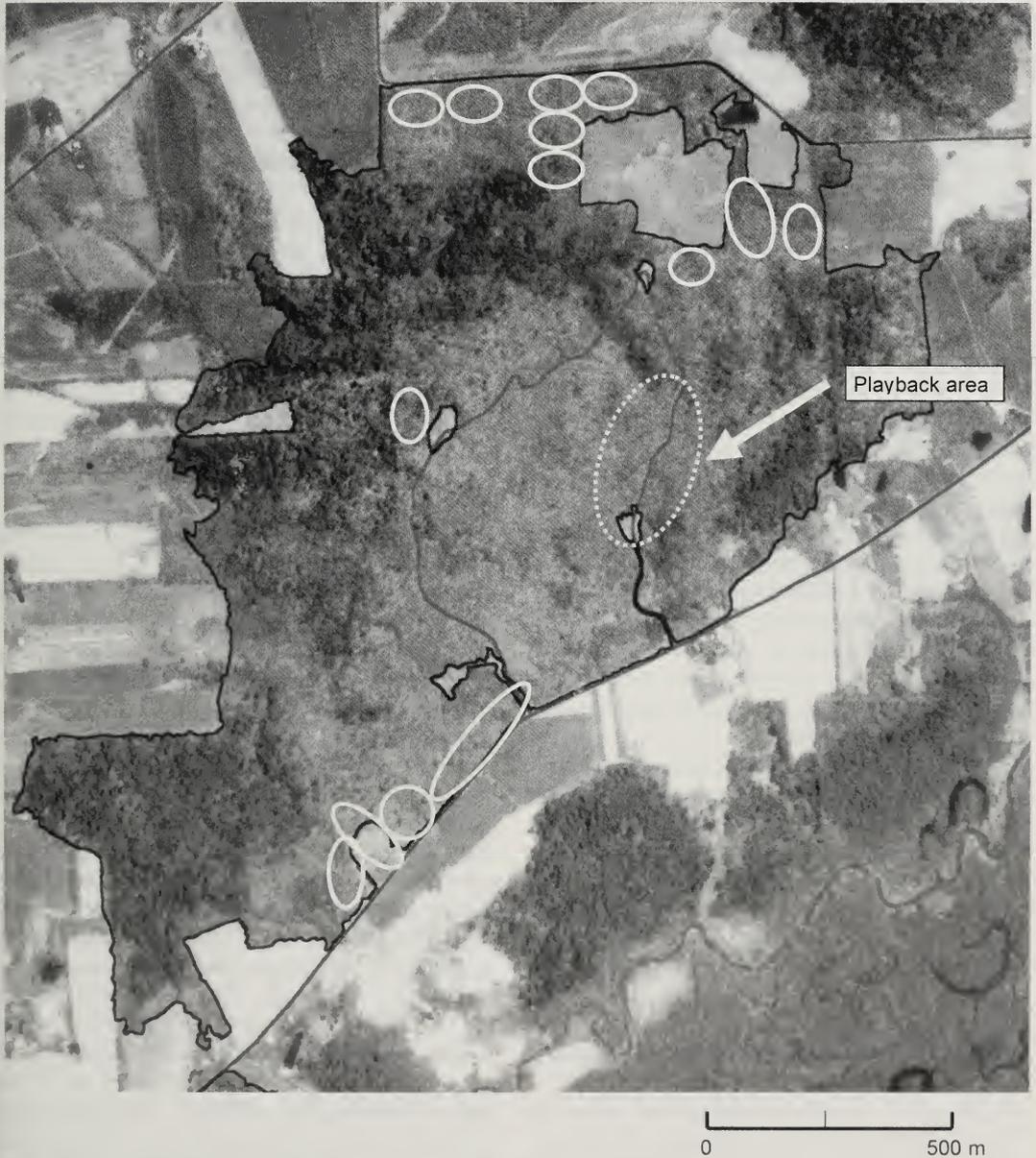


FIG. 1. Aerial photo of the Hemlock Hill Biological Research Area (HHBRA bordered in black) in northwestern Pennsylvania ( $41^{\circ} 4' N$ ,  $79^{\circ} 5' W$ ), taken in April 1994. Dark areas are dominated by eastern hemlock (*Tsuga canadensis*); deciduous forest is light-colored because trees were not yet leafed out. The entire Ovenbird population at the site ( $n = 14$  pairs; territories depicted by white ovals) occurs in edge habitat. The 18-ha song playback area, indicated by the dashed oval, is in the interior of mature deciduous forest. A path can be seen going through the playback area and continuing in a loop through the forest. The four Ovenbird territories at the southern boundary abut a paved road bordering HHBRA; there are hay fields to the south of the road. No Ovenbirds have bred within the playback area over the past 33 years (1971 through 2003).

1994, Morton et al. 1998). Each year, 9–14 Ovenbird territories were detected at the same sites and only at forest edges (Fig. 1). To show differences in forest maturity, I established transects (50 m long) between two grid points to count and measure tree species and trunk diameters in Ovenbird territories ( $n = 10$ ) and in areas not used by Ovenbirds ( $n = 7$ ). All trees  $>5$  cm diameter at breast height (dbh) and within 2 m of the transect line were tallied.

*Hypotheses.*—The 33 years of censuses at HHBRA showed that Ovenbirds bred in edge habitat in preference to forest interior. During this time, not a single breeding territory was located within the forest interior. With this background, in 2001–2003, I studied use of edge habitat by Ovenbirds at HHBRA in more detail, with the goal of testing why they might avoid forest-interior habitat. I tested several hypotheses: (1) Ovenbirds at HHBRA are nonbreeding, non-pairing transients; (2) food abundance is greater in edge habitat than in forest interior; and (3) Ovenbirds avoid using habitat with dense populations of eastern chipmunk, a potential predator.

I tested the first hypothesis by color banding all breeding males and mapping their territories each year. The pairing status of all males in the study area was assessed 5–10 times each year between late May and late June for the presence of mates. Returns by birds in subsequent years and acquiring mates and nesting would indicate that the Ovenbirds are not nonbreeding, non-pairing transients, but are breeders.

To test hypothesis 2, in 2003 I sampled litter depth on territories and compared those samples with random samples from the forest interior (unused habitat) following the protocol of Burke and Nol (1998). Those authors found that litter depth is positively correlated with food abundance for Ovenbirds, a ground-foraging species. I sampled litter depth at 10-m intervals along nine 50-m transects between grid points, six of which encompassed Ovenbird territories and three of which—randomly chosen—crossed forest-interior areas without breeding Ovenbirds.

Chipmunks are common forest and edge inhabitants in the research area and are predators on eggs, nestlings, and fledglings (Hill and Gates 1988, Reitsma et al. 1990, Fenske-

Crawford and Niemi 1997, King et al. 1998, Maier and DeGraaf 2000, Zegers et al. 2000). To test hypothesis 3, whether Ovenbirds avoid areas with many chipmunks, I assessed chipmunk prevalence by walking to a randomly chosen grid point, either within or outside of an Ovenbird territory. Once positioned there, I sat quietly on a folding chair and after 2 min began recording the time it took to detect (hear or see) a chipmunk within a radius of 25 m during the next 10 min. If no chipmunk was detected, a time of 600 sec was recorded. All chipmunk surveys were conducted on sunny, warm days from 09:30 to 11:30 EDT in July of 2001 and 2003. On- and off-territory chipmunk detection trials were paired for date, weather, and time of day. All on-territory trials were conducted in forest-edge habitat because there were no Ovenbird territories in the forest interior. Off-territory trials were either in forest interior within 200 m of an Ovenbird territory, or in an edge area unoccupied by Ovenbirds.

*Playback study.*—I conducted daily dawn-to-dusk playbacks of Ovenbird songs to induce settlement by simulating territorial occupation (Reed et al. 1999). A series of high-quality songs were recorded at normal singing cadence from one male breeding on the study site in 1985. Songs were played back continuously, except during heavy rains, from three Johnny Stewart Mini Wildlife Callers on 6-min TDK endless loop cassettes. Callers were located 100 m apart in the interior of mature deciduous forest. The broadcast covered an area of 18 ha (Fig. 1), determined by mapping points at distances from the speakers where the playback could just be detected by a human observer. The speaker locations were chosen because the mature forest surrounding them had no breeding Ovenbirds during the past 3 decades, and a trail allowed access. Speakers were placed 100 m apart, rather than randomly throughout the study area, because Ovenbird territories are clumped and a single, isolated speaker would not depict this normal situation. I conducted playback trials over two seasons. The first (16 July to 31 August 2001), consisted of 201 hr, 45 min of playback averaging 7 hr, 45 min per day and was designed to attract birds that were prospecting for territories for the next breeding season, spring 2002. The second series (24 April to 20 May

2003) ended when all traditional territories were filled and males were paired and nesting. This series consisted of 183 hr, 43 min of playback averaging 7 hr, 43 min per day, beginning at 06:00. Here, I wanted to see whether spring migrants could be attracted to settle immediately for the 2003 breeding season. Two-hr surveys for Ovenbirds that may have settled in response to playbacks were conducted every other day during the territory acquisition period (5 May to mid-June) in 2002 and 2003.

## RESULTS

Ovenbird reproductive and pairing success varies among regions and studies. Edge habitat may be used, but with less reproductive success than in forest interior; it may be avoided; or, there may be little difference in nesting and pairing success (Table 1). Only at HHBRA and surrounding areas have Ovenbirds entirely avoided nesting in forest interior. I will first describe the situation at HHBRA and then report on the hypotheses testing mentioned above.

For 33 years, no Ovenbird territories occurred in the interior of the mature deciduous forest (Fig. 1). Instead, territories bordered roads, fields, and on one occasion in 2001, a large clearing for a gas well adjacent to a new clear-cut in the forest. Occupied areas were former agricultural fields abandoned in the 1950s and regrown with aspens (*Populus grandidentata* and *P. tremuloides*), American elms (*Ulmus americana*), and red maples (*Acer rubrum*).

On the ten 50-m transects through Ovenbird territories, there was a mean of 4.4 tree species and  $15.2 \pm 5.9$  SD individual trees that averaged  $13.7 \pm 1.0$  cm in dbh. The seven transects in interior forest had a mean of 6.3 tree species and  $15.5 \pm 2.5$  individual trees that averaged  $18.9 \pm 12.8$  cm in dbh. American beech (*Fagus americana*), hop hornbeam (*Ostrya carpinifolia*), American hornbeam (*Carpinus caroliniana*), and northern red oak (*Quercus borealis*) were found only in the forest-interior transects.

*Transient versus breeding adults.*—Annual return rates for banded males ( $n = 14$  territories) were 67% in 2002 and 62% in 2003, within the normal range of return rates for male Ovenbirds; 85% were after-second-year

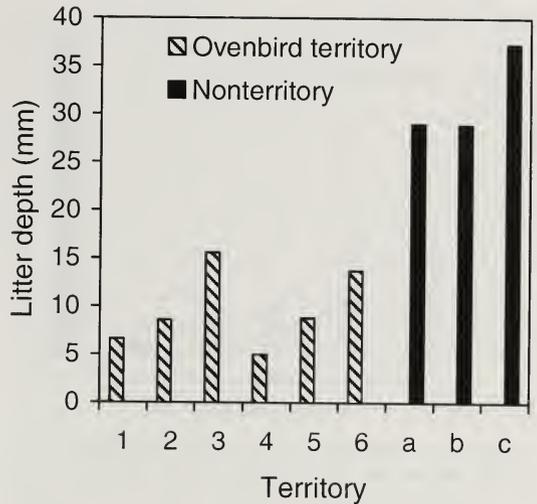


FIG. 2. Mean litter depth along 50-m transects (sampled every 10 m) in six different Ovenbird territories (1–6) and along three randomly placed forest-interior transects (a–c), northwestern Pennsylvania, 2003.

(ASY) birds. During the 2001–2003 study period, most males (86%) were paired—also within the normal range for forest-interior nesting birds in other studies (reviewed in Sabine et al. 1996, Burke and Nol 2001). I did not obtain information on breeding success, but young fledged successfully from four of four nests that were found incidentally. It is clear that these edge-inhabiting Ovenbirds were not transients, but were breeding adults that also had high pairing success and return rates.

*Food abundance in edge habitat versus forest interior.*—Mean litter depth was lower in Ovenbird territories ( $1.64 \text{ cm} \pm 1.34$ ) than it was in forest-interior habitat ( $3.17 \text{ cm} \pm 1.12$ ; Mann-Whitney test,  $z = -4.95$ ,  $P < 0.001$ ; Fig. 2). At HHBRA, litter depth in Ovenbird territories was less than that found on any territories in Ontario (Burke and Nol 1998); the same methods were used in both studies. In my forest-interior sample, litter depth (3.17 cm) was approximately the same as that found in Burke and Nol's (1998) most preferred nesting sites in large forest tracts. Insofar as litter depth is associated with food richness and nest-site preference in Ovenbirds (Burke and Nol 1998), we can reject the hypothesis that edge habitat at HHBRA offers more food

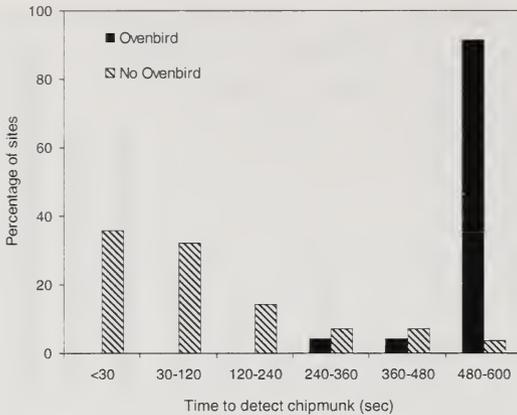


FIG. 3. Time (sec) to detect a chipmunk in the forest interior, unoccupied by Ovenbirds (hatched bars,  $n = 28$ ), compared with the time to detect a chipmunk within Ovenbird territories (black bars,  $n = 20$ ), north-western Pennsylvania, July 2001 and 2003. The maximum time allowed per point for chipmunk detection was 10 min. Chipmunks were rarely detected on Ovenbird territories but were abundant in forest interior.

and is more attractive to Ovenbirds than interior forest.

*Chipmunk populations on and off Ovenbird territories.*—Chipmunk presence was much greater off Ovenbird territories for each of the 2 years and for both years combined (Mann-Whitney test,  $z = 4.87$ ,  $P < 0.001$ ; Fig. 3). The average time to detect a chipmunk was only 2.1 min outside of Ovenbird territories, and chipmunks were found on 97% of the off-territory surveys. On Ovenbird territories, chipmunks were detected during only 3 of 21 surveys (14%) and it took an average of 7.2 min to detect them. Low chipmunk presence was not characteristic of all edge habitats at HHBRA and most edge did not hold Ovenbird territories (Fig. 1). In edge habitat not occupied by Ovenbirds ( $n = 5$  surveys, randomly selected), it took an average of 66 sec to detect Chipmunks, similar to detection times in the forest-interior habitat unused by Ovenbirds. On one territory, occupied during 2001 and 2002, no chipmunks were observed in the 10-min surveys on it. This territory was unoccupied in 2003, and a survey then resulted in chipmunks detected in 5 min, 48 sec.

*Playback study to induce Ovenbird settlement in forest interior.*—Neither the late-summer nor the spring playbacks induced Ovenbirds to establish territories in the 18-ha for-

est-interior area (Fig. 1). Individuals were occasionally observed in the playback area during the spring playback series, but none sang or remained. Instead, territories were re-occupied in the traditional edge areas.

## DISCUSSION

If one studied Ovenbirds only in north-western Pennsylvania, their habitat and behavior would be described as “forest edge; avoids mature interior forest!” This point highlights the need for assessing habitat use in many areas throughout a species’ range. For 33 years, Ovenbirds at HHBRA and the surrounding area have not settled in the interior of mature deciduous forest, despite low Ovenbird density and an abundance of what is usually considered “preferred” interior habitat. Although atypical, it may indicate that Ovenbirds are using nonhabitat cues when making decisions about whether or not to settle. An attempt to use playbacks to stimulate Ovenbird settlement in their preferred habitat at HHBRA failed. Summer playbacks failed to attract prospecting birds to settle the next breeding season and spring playbacks failed to induce settlement as well—although lone individuals were seen near the active playback speakers on several occasions.

The hypothesis that chipmunks—predators upon eggs, nestlings, and fledglings—deterred Ovenbirds from settling was supported. Chipmunks were nearly absent from Ovenbird territories during the 3-year study, but were abundant in the forest interior. It is possible that the Ovenbird territories at HHBRA are in edge habitats because some edge areas have low chipmunk numbers. If this is true, then the reasons for low chipmunk numbers should be perennial in the occupied edges; this appears to be the case. Chipmunks require an extensive burrow system for food storage, winter survival, and reproduction, but all Ovenbird-occupied edges were damp due to the presence of springs and poor drainage conditions; they also contained no large trees, whose root systems provide burrow support (Elliott 1978). In contrast, edges that supported chipmunk populations were drier and had large trees along former fence lines. Chipmunks are always common or abundant in our area (I have not recorded any year in which they were uncommon), perhaps due to the

abundance of both sugar (*Acer saccharum*) and red maples, trees that produce plentiful seed crops each year in fall and spring, respectively.

Could chipmunks be involved in habitat choice by Ovenbirds? As ground nesters and foragers, Ovenbirds are both particularly vulnerable to discovery by chipmunks and able to assess chipmunk density by directly encountering them during foraging or nest-site searching. The fact that Ovenbirds have an unusually short nestling period (8 days; Hann 1937) suggests that this species is under intense predation pressure (Bosque and Bosque 1995). Ovenbirds probably use litter depth (Burke and Nol 1998), as influenced by edaphic conditions (Smith 1977, Gibbs and Faaborg 1990, Blake et al. 1994), as a cue. Perhaps these direct habitat cues can be overshadowed by an assessment of chipmunk density. If so, then Ovenbirds at HHBRA might eschew forest interior there, where chipmunks are perennially common to abundant (ESM pers. obs.). As well, Ovenbird avoidance of chipmunks might have influenced the failure of playbacks to stimulate Ovenbirds to settle in the mature forest playback site (assuming they would respond to playbacks in the absence of chipmunks).

Some other ground-nesting species vulnerable to chipmunk predation also appear to choose nest sites that are chipmunk-free. For example, Dark-eyed Juncos (*Junco hyemalis*) and Louisiana Waterthrushes (*Seiurus motacilla*) place their nests only in recesses of vertical root balls of fallen trees (ESM pers. obs.). On the other hand, some forest ground nesters, such as Canada Warbler (*Wilsonia canadensis*), Black-and-white Warbler (*Mniotilta varia*), and Hermit Thrush (*Catharus guttatus*), do not exhibit this possible chipmunk avoidance ploy in their nest placement and are potential, but absent, breeders at HHBRA (ESM pers. obs.). Forstmeier and Weiss (2004) showed that Dusky Warblers (*Phylloscopus fuscatus*) exhibited adaptive plasticity in their nest-site selection. This tundra-inhabiting species places nests in safer and higher positions, at the expense of better microclimate and access to food, when Siberian chipmunk (*Tamias sibiricus*) populations are high. Forstmeier and Weiss (2004) suggested that Dusky Warblers, although short lived, are ca-

pable of assessing chipmunk numbers and selecting nests sites accordingly.

The evidence presented here on the importance of chipmunk activity precluding Ovenbirds from settling suggests the need for further experimental work. Future experiments could entail (1) removing chipmunks and then trying to attract Ovenbirds using playbacks, or (2) enticing chipmunks to invade traditional Ovenbird territories through food provisioning—and testing the prediction that Ovenbirds would no longer settle there. By altering chipmunk presence/absence, any definitive response in Ovenbird settlement would provide additional evidence that chipmunks afford cues to Ovenbirds when choosing nesting habitats.

The importance of looking for general, simple cues to habitat selection is clear. However, nearly all studies of habitat-selection cues have been of temperate zone birds whose territoriality coincides with reproduction. Avenues of habitat selection in tropical birds with yearlong territories, where biotic interactions are features of habitat requirements, await discovery. Mixed-species flocks or ant/acacia mutualisms are examples (Janzen 1969, Terborgh 1985, Marra and Remsen 1997, Stutchbury and Morton 2001). Habitat studies of birds should proceed beyond general descriptions, such as “forest interior” or “area sensitive,” for these terms may constrain, rather than enhance, explanations of habitat use (Villard 1998).

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## AVIAN FRUGIVORY ON A GAP-SPECIALIST, THE RED ELDERBERRY (*SAMBUCUS RACEMOSA*)

BRIDGET J. M. STUTCHBURY,<sup>1,3</sup> BIANCA CAPUANO,<sup>1</sup> AND GAIL S. FRASER<sup>2</sup>

**ABSTRACT.**—In the temperate zone, few plants produce fruit during the peak of the avian breeding season when arthropods are abundant. This study examined avian frugivory on red elderberry (*Sambucus racemosa pubens*), a gap-specialist that fruits in late June and early July. First, we videotaped fruiting elderberry plants ( $n = 67$  hr) within a forest to determine which avian species ate elderberry fruit. The birds that fed most frequently on red elderberry fruits were Scarlet Tanagers (*Piranga olivacea*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*). We then analyzed radiotelemetry data for Scarlet Tanagers to determine (1) whether tanagers shifted their territories when elderberry was in fruit, and (2) whether tanagers traveled long distances off territory to visit fruiting elderberry. During the fruiting period, male tanagers shifted their home ranges and spent more time near elderberry bushes; however, they left their territories only 0.25 times per hr and moved an average of only 115 m during trips off territory. These results suggest that while tanagers do focus their activity near fruiting elderberry, they do not leave their territories regularly to find fruit. Received 23 November 2004, accepted 18 July 2005.

In the temperate zone, few plants produce fruit during the avian breeding season (Thompson and Willson 1979, Wheelwright 1988), and the typical pattern is for temperate zone plants to fruit in late summer and early fall (Morton 1973). Only a small fraction of the breeding bird community is even partly frugivorous, largely because of the high abundance and protein content of arthropods (although we note that many insectivorous migrants do eat fruit in the nonbreeding season). Little is known about the importance of fruit to temperate breeding birds (McCarty et al. 2002), or about the movements of territorial bird species in response to early-fruiting plants (Gorchov 1988).

Red elderberry (*Sambucus racemosa pubens*), typically found in forest gaps, is among the earliest woody plants to fruit in the northeastern region of the United States (Stiles 1980) and is available to forest birds while they are still nesting. In this study, we videotaped ripe elderberry shrubs to quantify which avian species fed on elderberry fruit and the rate at which plants were visited. We also analyzed radiotelemetry movements of one key species that eats elderberry, the Scarlet Tanager (*Piranga olivacea*)—to determine whether it shifts its territory use in response

to fruiting elderberry or makes long distance movements off territory in search of fruit.

### METHODS

**Study area.**—From 2000 to 2003, we studied avian frugivory on red elderberry at the Hemlock Hill Biological Research Area (41° 46' N, 79° 56' W), a 150-ha mixed forest in Crawford County, northwestern Pennsylvania. The fruiting period for elderberry was between mid-June and mid-July, although individual plants were sometimes depleted of fruit within 7–10 days of ripening in mid- or late June. We searched the study site for elderberry plants and found 54 different plants (0.36/ha) at 19 different sites (defined as >50 m apart; 0.13 sites/ha). Fruiting plants typically had 20–50 clusters of fruit per plant (mean = 24, SD = 25.8,  $n = 49$  plants), with about 200 individual fruits per cluster. Fruits are brilliant red, small (3–5 mm diameter; 0.05 g wet mass), and have a relatively high-energy content (68.8 kcal/100 g; Usui et al. 1994).

**Bird visits and bird surveys.**—We selected medium- or large-sized elderberry plants for videotaping; for a subset of these plants, the mean number of fruit clusters was 46 (SD = 33, range = 8–105 clusters per plant,  $n = 11$ ). Some sites contained several adjacent elderberry plants that were videotaped separately, but were considered the same site because presumably the same individual birds fed on adjacent elderberry plants. We videotaped 14 different sites, 3 of which were taped in 2 dif-

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TABLE 1. The occurrence of videotaped species foraging on red elderberry fruit ( $n = 17$  sites) from mid-June to mid-July in northwestern Pennsylvania, and the detection of those species (percentage of sites) during bird surveys in early July 2003 at elderberry sites ( $n = 14$ ). Foraging observations are based on the percentage of sites at which the species was videotaped and percentage of all bird visits ( $n = 106$ ) to elderberry represented by that species.

Species	Elderberry foraging		Bird surveys
	% sites	% visits	
Scarlet Tanager ( <i>Piranga olivacea</i> )	35.3	45.3	64%
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	23.5	22.6	36%
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	17.6	6.6	100%
Veery ( <i>Catharus fuscescens</i> )	17.6	7.5	50%
American Robin ( <i>Turdus migratorius</i> )	5.9	1.9	29%
Wood Thrush ( <i>Hylocichla mustelina</i> )	5.9	0.9	79%
Northern Cardinal ( <i>Cardinalis cardinalis</i> )	5.9	1.9	71%
Gray Catbird ( <i>Dumetella carolinensis</i> )	5.9	5.7	21%
Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )	5.9	3.8	14%
Downy Woodpecker ( <i>Picoides pubescens</i> )	5.9	1.9	—
Yellow-bellied Sapsucker ( <i>Sphyrapicus varius</i> )	5.9	0.9	—
Unidentified birds	29.4	8.5	

ferent years, yielding a sample size of 17 sites. Video cameras (Sony Hi-8) were positioned so that most or all of one fruiting plant could be observed, and we collected 1–4 hr of tape per taping session depending on the weather and the camera's capability. We videotaped plants between 09:00 and 17:00 EDT, only during dry weather. Tapes were later viewed on a television screen, and bird species were identified visually and/or by their call notes. We noted the time each bird spent foraging before departing from an elderberry plant. We could not accurately count the number of fruits eaten because our view of an individual was often blocked by vegetation as it foraged.

To assess the abundance of frugivorous species relative to their visitation to elderberry, in 2003 we surveyed 14 elderberry sites for the presence or absence of frugivores. At each site where fruiting elderberry was present, we listened for singing birds within 50 m of the elderberry site for 10 min. We then played back 1 min of song, followed by 1 min of silence, for nine species of passerines that are partially frugivorous (Red-eyed Vireo, Wood Thrush, Veery, American Robin, Northern Cardinal, Scarlet Tanager, Rose-breasted Grosbeak, Gray Catbird, Eastern Towhee; see Table 1 for scientific names). Surveys were conducted once during morning (09:00–12:00), from 30 June to 3 July 2003.

**Radiotelemetry.**—In 2000 and 2001, we captured tanagers by using a playback system,

decoy, and mist nets and banded them with a federal band and a combination of individually identifiable color bands. Males ( $n = 10$ ) were fitted with a small (1.4 g), BD-2G radio transmitter (Holohil Systems, Carp, Ontario, Canada) that was attached with a figure-8 harness made of cotton embroidery thread (see Rappole and Tipton 1991). The transmitter and harness together weighed about 5% of adult body mass (30 g). Transmitter batteries lasted 8 weeks and the range was approximately 1.5 km. The study site had conspicuous grid marks every 50 m and the locations of males were recorded by noting the closest grid mark(s) whenever the bird moved. Movements off territory were defined as occurring when a male entered another male's territory (for known boundaries) or when males moved at least 100 m away from their own territory boundary.

Tanagers were tracked between 13 May and 30 June to study off-territory movements (Fraser and Stutchbury 2004) and to compare movements before versus after elderberry fruit was ripe. We radio-tracked tanagers for about 2 hr at a time, between 06:00 and 14:00, and followed males from a distance of about 30 m. Observations were not made during wet weather because the receiver was not waterproof. We mapped the location of all elderberry shrubs in the territories of radio-tagged males, and quantified the relationship between territory size, movements, and fruiting shrubs.

We had a total of 116 hr of radio-tracking data—46 hr during the pre-fruiting period (before 15 June) and 70 hr during the fruiting period (15 June–30 June). We had a minimum of 6 hr of tracking time for each male used in our analyses.

For seven males we used paired observations (6 hr pre-fruiting, 6 hr fruiting) and predicted that males would spend more time in an area with ripe elderberries than they would during the pre-fruiting period. We used two measurements during the pre-fruiting and fruiting periods to determine whether males were more likely to include ripe elderberry patches during their movements: (1) the percent time spent within 25 m of an elderberry shrub out of the total time tracked, and (2) the total number of elderberry shrubs contained within the male's home range in each tracking session. Both comparisons were tested with a one-tailed, Wilcoxon paired signed-ranks test.

## RESULTS

*Birds that ate elderberry fruit.*—From videotapes, we identified 11 bird species and one eastern chipmunk (*Tamias striatus*) foraging on ripe elderberry (Table 1). We were unable to identify the bird species in only 8.5% of visits seen on the videotapes. The Scarlet Tanager was the species observed most often on elderberry plants; tanagers were seen at 35.3% of sites, and accounted for 45.3% of all bird visits to elderberry. The Rose-breasted Grosbeak was the second most common visitor to elderberry (22.6% of visits). The occurrence of a given species feeding on elderberry did not correspond closely to the species' prevalence—as assessed during our site surveys (Table 1). The percentage of sites visited ( $r_s = 0.275$ ,  $n = 9$ ,  $P = 0.24$ ) and the percentage of visits ( $r_s = 0.05$ ,  $n = 9$ ,  $P = 0.45$ ) were not significantly correlated with the percentage of surveys on which the species was detected. For instance, Red-eyed Vireos and Northern Cardinals were very common birds at our study site (and responded readily to playback) but were rarely seen visiting elderberry shrubs. In contrast, the low level of frugivory by American Robins, Gray Catbirds, and Eastern Towhees likely did reflect the low abundance of these species in the forest. The Rose-breasted Grosbeak was often seen feeding on elderberry but was detected on only

36% of surveys, which may reflect a low detection ability for this species due to low song rates and weak responses to playback.

The rate of visits by frugivores was highly variable between sites. For sites that were observed for at least 3 hr ( $n = 10$ ), we observed no visits at three sites, <1 visit/hr at three sites, 1–5 visits/hr at two sites, and >5 visits/hr at two sites. One elderberry plant was visited by birds 29 times over a 3-hr period, although this plant did not have an unusually large amount of fruit (84 clusters). For 2003, when we estimated fruit crop, there was no correlation between the total number of fruit clusters per site and the visit rate/hr at that site ( $r_s = 0.07$ ,  $n = 7$ ,  $P = 0.86$ ).

The average time spent on elderberry per visit was 59.4 sec (SD = 55.2, range = 5–260 sec,  $n = 54$  visits). Most birds consumed the small fruits while on the elderberry plant, although several species were occasionally observed feeding elderberries to their fledglings or departing with fruit in their bills (Scarlet Tanager, Rose-breasted Grosbeak, Veery, American Robin).

*Elderberry effect on tanager movements and territory use.*—We radio-tracked seven paired males during both the pre-fruiting and fruiting periods to determine whether they shift their home-range use in response to the presence of ripe elderberry fruit. During the fruiting period, males spent significantly more time <25 m from elderberry ( $12.8\% \pm 0.14$  SD) than they did during the pre-fruiting period ( $4.0\% \pm 0.075$ ;  $Z = -1.99$ ,  $n = 7$ ,  $P = 0.023$ ). There also was a strong but nonsignificant trend ( $Z = -1.47$ ,  $n = 7$ ,  $P = 0.068$ ) among males to shift their home ranges to include more elderberry shrubs during the fruiting period ( $1.71 \pm 1.5$ ) compared with the pre-fruiting period ( $0.71 \pm 0.76$ ). Territory size (ha) did not change significantly between periods (pre-fruiting:  $0.64 \pm 0.27$ , fruiting:  $0.94 \pm 0.60$ ;  $Z = -1.014$ ,  $n = 7$ ,  $P = 0.16$ ).

Eight of 10 males left their territories during the fruiting period, although the mean rate of off-territory forays was low ( $0.25$  trips/hr  $\pm 0.21$  SD). In most cases, when males did leave their territories, they went only  $115 \text{ m} \pm 124$  ( $n = 8$  trips) beyond their territory boundaries—roughly equivalent to the diameter of one tanager territory—and were not observed feeding on elderberry. We observed

only one male travel far (300 m) off territory to an area of ripe elderberry. In the 70.2 hr of tracking during the fruiting period, we observed 2 of the 10 radio-tagged males foraging on elderberry. In both cases, their mates (not radio-tagged) also were observed foraging on berries.

## DISCUSSION

We observed 11 different species of birds feeding on elderberry. Of 33 passerine species that regularly breed in the forest at this study site (BJMS pers. obs.), 9 species were observed feeding on fruit, and all were already known to be partially frugivorous during the breeding season.

In some instances, we recorded high visitation rates to individual plants (10 visits/hr), but for most plants there were no, or only several, visits by birds each hour. Nevertheless, most plants were stripped of fruit by mid-July, suggesting that at some point birds (we assume) did consume the fruit. Denslow (1987) found that fruit removal rate (number of fruits removed per day) of red elderberry shrubs was significantly higher for isolated plants with large crops and for those with high sugar content in the fruit. We found no correlation between number of fruit clusters per site and bird visitation rate, although our sample sizes were modest. For instance, one site with nine different elderberry shrubs and 198 fruit clusters was not visited in 3.5 hr of observation. Another site had only a single elderberry plant with 84 fruit clusters, yet it was visited 9.6 times per hr.

The occurrence of a given species foraging on elderberry did not closely correspond to its prevalence in the forest (Table 1). Wood Thrushes were rarely seen on elderberry shrubs, despite this species being detected at 80% of elderberry sites during bird censuses. Similarly, Red-eyed Vireos and Northern Cardinals were present at most elderberry sites but represented only a small fraction of all bird visits to elderberry shrubs. The species-specific use of elderberry fruit could reflect differences in availability of insect prey to birds with different bill morphologies and foraging substrates, and hence the relative value of the fruit at a time of year when many adults are feeding offspring.

Almost half the visits to elderberry during

our videotaping were made by Scarlet Tanagers. Although male tanagers did not make long trips off territory to find fruit, they did spend more time near elderberry when it was ripe. However, stomach content analysis of forest thrushes revealed relatively low fruit content in June and July (White and Stiles 1990), and the same may be true for tanagers (Mowbray 1999). The low fruit content in the diet could reflect the low number of fruiting species available at that time of year and the low density of these plants. In our study area, the density of elderberry sites was only 0.13/ha and many tanager pairs had no elderberry plants on their territories. We have observed tanagers feeding elderberries to older nestlings and fledglings, but it is not known whether feeding fruit to young increases the reproductive success of the parents.

Our results have implications for understanding seed dispersal by this early-fruiting plant. One of the potential costs of early fruiting is limited seed dispersal due to territoriality during the peak breeding season of birds (Morton 1973, Willson and Thompson 1982). However, Gorchov (1988) found that dispersal of one early-fruiting species, *Amelanchier arborea*, was not restricted by territoriality, because the main avian disperser was the Cedar Waxwing (*Bombycilla cedrorum*), which forages in flocks. Our results suggest that dispersal distance of red elderberry within a forest may indeed be limited by territoriality because male Scarlet Tanagers did not regularly commute off territory to search for fruit. Most of the birds that ate elderberry (Table 1) defend all-purpose territories and may be similarly constrained. Although male (and female) tanagers do often leave their territories after breeding (Vega Rivera et al. 2003), this occurs later in summer after the main fruiting period of red elderberry. Red elderberry is a gap-specialist, but it is not necessarily disadvantaged by dispersal within a bird's territory. What may be more important than distance *per se* is that the seeds are dispersed to a favorable site (e.g., Wenny and Levey 1998)—in this case, another gap within the territory—or are dispersed to sites within the forest where they can wait for a gap to form above them.

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## BIRD COMMUNITIES AFTER BLOWDOWN IN A LATE-SUCCESSIONAL GREAT LAKES SPRUCE-FIR FOREST

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**ABSTRACT.**—In 2001 and 2002, we inventoried the bird communities and vegetation of two 6.25-ha plots in a late-successional spruce-fir (*Picea mariana*–*Abies balsamea*) forest of northern Minnesota that was severely disturbed by a 1999 windstorm. We compared these results with those from two nearby plots that were largely unaffected by the storm. Using vegetation data collected from one of the two plots in each location before the disturbance in 1996 and 1998, we examined similarities between plots before and after the storm. The most significant effect of the storm on vegetation was a  $\geq 80\%$  decrease in tree cover and a  $> 100\%$  increase in shrub-layer structure because of trees that were tipped over or snapped off. Of 30 territorial bird species, 9 held territories exclusively in the blowdown, while 2 held territories exclusively in the control. By foraging guild, 10 of 11 (91%) species of ground-brush foragers had more territory cover in the blowdown, while 7 of 13 (54%) species of tree-foliage searchers had more territory cover in the control. Black-and-white Warbler (*Mniotilta varia*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Mourning Warbler (*Oporornis philadelphia*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), and Red-eyed Vireo (*Vireo olivaceus*) had significantly ( $P < 0.05$ ) more territory cover in the blowdown, whereas Blackburnian Warbler (*Dendroica fusca*), Golden-crowned Kinglet (*Regulus satrapa*), and Yellow-rumped Warbler (*Dendroica coronata*) had more territory cover in the control. Canonical correspondence analysis revealed that differences in avian territory cover were primarily attributable to changes in vegetation structure, in particular the increase of structural debris on the ground and the reduction in tree canopy, occurring because of the wind. Received 25 October 2004, accepted 30 August 2005.

Forest composition and structure in the Upper Great Lakes region is greatly influenced by disturbances, primarily fire, insect outbreaks, logging, and wind (Van Wagner and Methven 1978, Bonan and Shugart 1989, Bergeron 1991, Drapeau et al. 2000). Although the most prevalent natural disturbances in this region are fire and insects, large-scale wind events that significantly reduce the canopy are believed to occur with average return intervals of 1,000 years or more (Frelich and Reich 1996, Larson and Waldron 2000, Frelich 2002). A number of studies have examined the effects of disturbances such as fire and logging on avian communities in the Upper Great Lakes region (Apfelbaum and Haney 1986, Schulte and Niemi 1998, Drapeau et al. 2000); however, despite its known impact on vegetation structure and composition (Frelich and Reich 1996), few researchers have examined the effects of wind (Smith and Dallman 1996, Dyer and Baird-Philip 1997).

On 4 July 1999, a microburst—known as a derecho, and characterized by straight-line

winds in excess of 145 km/hr—disturbed approximately 200,000 ha in northeastern Minnesota (USDA Forest Service 2002). We documented the effects of severe wind disturbance by comparing post-disturbance vegetation and bird communities on two blowdown plots with two nearby control plots that had the same disturbance history and vegetation structure before the storm. Because bird species composition is closely related to habitat structure (Karr and Roth 1971, Willson 1974, Niemi and Hanowski 1984, Pearman 2002), and because the wind reduced tree cover by more than 80%, with a corresponding increase in shrub-layer structure and coarse woody debris from tipped trees and snapped tree-tops, we expected a community shift from one dominated by tree-foliage searchers to one dominated by ground-brush foragers. We expected responses similar to those following fire (Apfelbaum and Haney 1981, Morissette et al. 2002) and, in some cases, timber harvesting (Hobson and Schieck 1999, Lohr et al. 2002).

### METHODS

We conducted our study in a 200-year-old black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) forest that originated from

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an 1801 stand-replacing wildfire (M. L. Heinzelman pers. comm.) in northeastern Minnesota's Superior National Forest (Fig. 1). Two blowdown study plots were located on Seagull Lake (48° 07' N, 90° 54' W) and two control plots, minimally affected by the 4 July 1999 storm, were located near Red Rock Bay (Saganaga Lake), approximately 10 km to the northwest of Seagull Lake. Each 250 × 250-m (6.25 ha) study plot, surrounded by a 25-m buffer zone to reduce the effects of edge, was subdivided with flagging into a grid of 50 × 50-m cells. Using previously collected data from one of the blowdown plots (1996) and one of the control plots (1998), we employed a BACI design (Before, After, Control, Impact; Stewart-Oaten et al. 1986, Irons et al. 2000, Stewart-Oaten and Bence 2001) to better illustrate similarities between plots before the disturbance, and changes occurring because of the windstorm. We did not use a BACI design to analyze our bird data, however, because the annual variation in bird populations is unpredictable (Blake et al. 1994, Collins 2001) and our pre-disturbance avian surveys were conducted in different years.

Post-blowdown vegetation surveys were conducted in 2001 and again in 2002 along 50-m transects running through the center of 10 randomly selected grid cells in each of the four study plots ( $n = 4$  plots/year × 10 cells/plot × 2 years = 80). Using the same methodology, we surveyed vegetation in one of the pre-blowdown plots in 1996 and one of the control plots in 1998 ( $n = 2$  plots × 10 cells/plot = 20). Tree and shrub cover for each species were estimated using the line intercept method (Canfield 1941). Trees were defined as stems standing <45 degrees from vertical with a diameter at breast height (dbh) ≥ 5 cm. Shrubs were identified as all stems >1 m tall and <5 cm dbh or as live trees standing >45 degrees from vertical. Dead trees were considered coarse litter if standing >45 degrees from vertical and snags if standing <45 degrees. After the storm, diameters of all stems >5 cm that crossed the 50-m intercept line were recorded and used to estimate the volume of coarse woody debris per unit area.

We estimated tree and shrub density by recording the number and diameter (rounded to the nearest 5 cm) of live and dead trees rooted within 1 m of either side of the transect and

the number of live and dead shrub stems within 1 m of the right side of the transect. We used five 1-m<sup>2</sup> circular plots centered at 5, 15, 25, 35, and 45 m along the transect line to estimate percent cover of herbs (height <1 m), exposed mineral (e.g., rock, bare soil), bryophytes, coarse litter (diameter >5 cm), and fine litter (diameter <5 cm).

We conducted bird surveys on each of the four plots once per morning for each of 5 days during May–mid-June 2001 and 2002. Surveys were performed using a modification of Kendeigh's flush-plot techniques (Kendeigh 1944, Apfelbaum and Haney 1986). Each survey was conducted by one or two experienced birders who plotted on data sheets all birds seen or heard from grid-cell vertices. Surveys, which were restricted to days without significant wind or rain, averaged about 6 person-hr, each designed to plot every territorial male using the area.

After the completion of all five daily surveys, bird locations for each plot were compiled onto summary sheets. Territories were delineated from clusters of survey registrations and other evidence of established territories, such as active nests, or adults carrying food or fecal sacs. We considered likely transients, or individuals with territories too large to determine with our method, as visitors (V) unless they were recorded in the same location on at least 3 of the 5 survey days.

*Data analyses.*—To address issues of spatial dependence within the vegetation dataset, we first eliminated repeatedly sampled grid cells while balancing sample sizes between years and plots. Of the 100 grid cells for which we had vegetation data, we retained 62 cells (10 pre-blowdown [1996], 10 pre-blowdown control [1998], 12 post-blowdown [2001], 11 post-blowdown control [2001], 9 post-blowdown [2002], 10 post-blowdown control [2002]) for further analysis. Next, we examined the resulting vegetation data for normality (Q-Q plot and Shapiro-Wilk tests) and homogeneity of variance (Levene's test) and transformed data according to Box-Cox plots (Box and Cox 1964) as necessary. Finally, we used a two-way analysis of variance (ANOVA) for each habitat variable ( $n = 19$ ) to examine differences based both on plot type (blowdown or control) and time (1996 or 1998, 2001, 2002). If the ANOVA yielded a

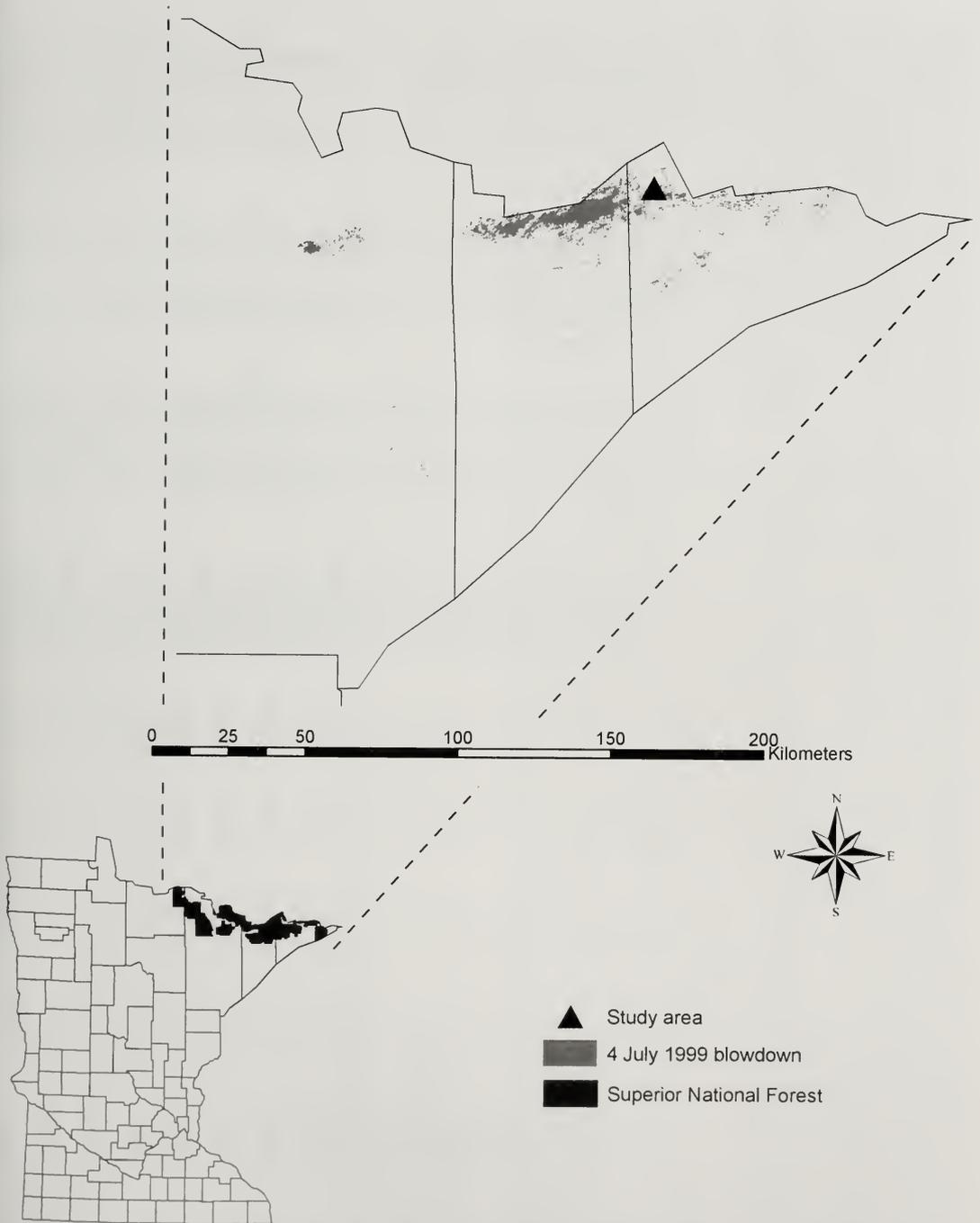


FIG. 1. Location of the study area and the blowdown area in northeastern Minnesota's Superior National Forest. The blowdown occurred 4 July 1999, a result of a >145 km/hr microburst.

TABLE 1. Mean vegetation characteristics ( $\pm$ SE) and outcomes of two-way ANOVA on 62 (31 control, 31 blowdown) 50-m transects before (1996 or 1998)<sup>a</sup> and after (2001, 2002) a catastrophic blowdown in a black spruce-balsam fir forest in the Superior National Forest, Minnesota. When ANOVA (site  $\times$  time) yielded a significant interaction ( $P < 0.05$ ), simple main effects analyses were conducted, followed by pairwise comparisons to examine differences between the blowdown and control plots. Asterisks indicate a significant difference (Bonferroni:  $\alpha = 0.025$ ) between plot types in the given year (column), while different capital letters indicate significant differences (Bonferroni:  $\alpha = 0.008$ ) between years in the given plot type (row). There were no significant differences between years for control plots. CBRYO = % bryophyte cover; CCOLIT = % coarse litter cover; CFILIT = % fine litter cover; CHERB = % herb cover; CMINRL = % mineral cover; CSHRB = % shrub cover; CSHRBD = % deciduous shrub cover; CSHRBE = % evergreen shrub cover; CTREE = % tree cover; CTREED = % deciduous tree cover; CTREEE = % evergreen tree cover; CVR = % shrub or tree cover; DEBRIS = coarse woody debris (m<sup>3</sup>); DEDDIA = dead tree diameter (cm); DEDSHR = dead shrub stems; DEDTRE = dead trees; LIVDIA = live tree diameter (cm); LIVSHR = live shrub stems; LIVTRE = live trees.

Vegetation variable	ANOVA						Mean				
	Site		Time		Site $\times$ Time		Pre-blowdown 1998 <sup>a</sup>		Post-blowdown 2001		Post-blowdown 2002
	F	P	F	P	F	P	Plot type				
CBRYO <sup>b,d</sup>	1.30	0.26	0.20	0.82	2.38	0.10	Control	39.3 $\pm$ 5.83	52.6 $\pm$ 6.91	34.6 $\pm$ 7.62	
							Blowdown	38.6 $\pm$ 5.65	29.7 $\pm$ 6.44	39.1 $\pm$ 8.60	
CCOLIT <sup>b,d</sup>	1.34	0.25	0.40	0.67	1.43	0.25	Control	12.0 $\pm$ 2.22	14.0 $\pm$ 3.12	14.3 $\pm$ 2.70	
							Blowdown	19.8 $\pm$ 3.10	16.0 $\pm$ 2.90	12.4 $\pm$ 1.94	
CFILIT <sup>d</sup>	0.89	0.35	5.48	0.007	0.77	0.47	Control	32.7 $\pm$ 2.96	57.4 $\pm$ 8.47	60.2 $\pm$ 7.00	
							Blowdown	47.0 $\pm$ 6.20	60.9 $\pm$ 7.64	57.8 $\pm$ 4.14	
CHERB <sup>d</sup>	0.52	0.47	0.67	0.52	1.43	0.25	Control	38.1 $\pm$ 5.34	28.9 $\pm$ 4.75	26.9 $\pm$ 3.79	
							Blowdown	27.7 $\pm$ 2.91	27.9 $\pm$ 3.43	31.0 $\pm$ 4.97	
CMINRL <sup>c,d</sup>	0.01	0.93	6.16	0.004	0.94	0.40	Control	3.0 $\pm$ 1.55	1.7 $\pm$ 0.71	6.0 $\pm$ 2.58	
							Blowdown	0.62 $\pm$ 0.30	2.3 $\pm$ 0.84	8.2 $\pm$ 2.89	
CSHRB <sup>d</sup>	7.74	0.007	4.17	0.021	3.29	0.045	Control	44.1 $\pm$ 5.06*	45.3 $\pm$ 3.96	42.8 $\pm$ 5.78	
							Blowdown	22.6 $\pm$ 2.04*A	46.5 $\pm$ 5.15B	32.2 $\pm$ 3.45AB	
CSHRBD <sup>d</sup>	3.14	0.082	6.75	0.002	0.26	0.77	Control	6.8 $\pm$ 2.12	18.3 $\pm$ 3.52	17.3 $\pm$ 6.13	
							Blowdown	11.1 $\pm$ 1.86	27.0 $\pm$ 4.03	21.2 $\pm$ 3.40	
CSHRBE <sup>d</sup>	36.71	<0.001	2.58	0.085	1.78	0.18	Control	34.1 $\pm$ 3.80	33.8 $\pm$ 4.09	31.2 $\pm$ 3.67	
							Blowdown	12.4 $\pm$ 2.10	23.9 $\pm$ 3.60	12.1 $\pm$ 1.76	
CTREEE <sup>b,d</sup>	11.37	0.001	11.71	<0.001	9.95	<0.001	Control	40.1 $\pm$ 4.38*	42.9 $\pm$ 5.47*	37.6 $\pm$ 6.08*	
							Blowdown	51.6 $\pm$ 3.75*A	23.4 $\pm$ 5.07*B	7.6 $\pm$ 3.23*B	
CTREED <sup>c,d</sup>	0.23	0.63	6.78	0.002	1.42	0.25	Control	19.0 $\pm$ 4.96	16.4 $\pm$ 5.90	10.3 $\pm$ 2.22	
							Blowdown	24.2 $\pm$ 3.45	14.0 $\pm$ 3.94	2.9 $\pm$ 2.74	
CTREEE <sup>b,d</sup>	16.32	<0.001	5.38	0.007	9.23	<0.001	Control	26.0 $\pm$ 2.26	32.0 $\pm$ 4.30*	29.1 $\pm$ 7.03*	
							Blowdown	33.1 $\pm$ 4.48A	10.5 $\pm$ 2.47*B	5.0 $\pm$ 1.43*B	
CVR <sup>d</sup>	13.71	<0.001	4.49	0.016	3.39	0.041	Control	67.7 $\pm$ 4.69	67.9 $\pm$ 4.87	66.1 $\pm$ 5.44*	
							Blowdown	62.8 $\pm$ 3.30A	58.6 $\pm$ 4.69A	37.6 $\pm$ 4.71*B	
DEBRIS <sup>b,f</sup>	14.94	<0.001	1.73	0.20	1.36	0.25	Control	no data	57.3 $\pm$ 12.35	33.6 $\pm$ 8.78	
							Blowdown	no data	93.3 $\pm$ 15.43	89.4 $\pm$ 14.05	
DEDDIA <sup>d</sup>	8.68	0.005	0.79	0.46	0.02	0.98	Control	10.8 $\pm$ 1.86	13.5 $\pm$ 1.82	14.7 $\pm$ 3.23	
							Blowdown	17.9 $\pm$ 2.22	20.0 $\pm$ 2.70	20.7 $\pm$ 3.68	
DEDSHR <sup>c,d</sup>	3.79	0.057	3.99	0.024	1.30	0.28	Control	6.1 $\pm$ 1.29	3.1 $\pm$ 0.81	2.0 $\pm$ 0.60	
							Blowdown	3.4 $\pm$ 1.22	1.3 $\pm$ 0.45	2.2 $\pm$ 0.89	

TABLE 1. Continued.

Vegetation variable	ANOVA						Mean							
	Site			Time			Site × Time		199x <sup>a</sup>		2001		2002	
	F	P	F	F	P	F	P	Pre-blowdown	Post-blowdown	Pre-blowdown	Post-blowdown	Pre-blowdown	Post-blowdown	
DEDTRE <sup>b,d</sup>	1.42	0.24	2.42	0.098	2.15	0.13	Control	4.3 ± 1.01	3.6 ± 1.17	4.3 ± 1.01	3.6 ± 1.17	4.3 ± 1.01	3.6 ± 1.17	
LIVDIA <sup>c</sup>	0.91	0.34	7.81	0.001	8.90	<0.001	Blowdown	2.2 ± 0.47	2.0 ± 0.37	2.2 ± 0.47	2.0 ± 0.37	2.2 ± 0.47	2.1 ± 0.59	
LIVSHR <sup>d</sup>	0.14	0.71	4.77	0.012	1.50	0.23	Control	11.4 ± 0.90*	11.6 ± 1.15*	11.4 ± 0.90*	11.6 ± 1.15*	11.4 ± 0.90*	11.7 ± 0.75*	
LIVTRE <sup>c,d</sup>	8.26	0.006	3.64	0.033	1.34	0.27	Blowdown	15.6 ± 1.49*A	8.8 ± 0.67*B	15.6 ± 1.49*A	8.8 ± 0.67*B	15.6 ± 1.49*A	7.9 ± 0.86*B	
							Control	44.5 ± 8.16	53.0 ± 8.54	44.5 ± 8.16	53.0 ± 8.54	44.5 ± 8.16	56.6 ± 10.9	
							Blowdown	24.1 ± 3.67	55.3 ± 10.31	24.1 ± 3.67	55.3 ± 10.31	24.1 ± 3.67	66.6 ± 9.25	
							Control	12.0 ± 2.09	10.8 ± 1.76	12.0 ± 2.09	10.8 ± 1.76	12.0 ± 2.09	12.1 ± 3.30	
							Blowdown	10.9 ± 1.82	5.8 ± 1.17	10.9 ± 1.82	5.8 ± 1.17	10.9 ± 1.82	3.3 ± 0.50	

<sup>a</sup> Data were collected in 1996 on the (pre-) blowdown plot, and in 1998 on the control plot.

<sup>b</sup> Data were transformed using square root.

<sup>c</sup> Data were transformed using natural log.

<sup>d</sup> Site df = 1.56; time df = 2.56; site × time df = 2.56.

<sup>e</sup> Site df = 1.55; time df = 2.55; site × time df = 2.55.

<sup>f</sup> Site df = 1.38; time df = 1.38; site × time df = 1.38.

significant interaction, indicating that the blowdown and control plots were changing differently with time, we conducted main effects analyses to examine both differences between plot type in a given year and differences between years within each plot type. To control for Type I error across the two simple main effects, we used a Bonferroni correction procedure (Winer et al. 1991) and set alpha for each simple main effect at 0.025. If the simple main effect (time) was significant, follow-up pairwise comparisons between 1996, 1998, 2001, and 2002 were performed using a Bonferroni-adjusted alpha set at 0.008 (0.025/3) to identify time periods of significant change.

Because we wanted to correlate bird presence with habitat characteristics, we analyzed our bird data at the same scale as the vegetation data (50 × 50-m grid cell), rather than at the 250 × 250-m plot level. This was accomplished by selecting 42 grid cells equally distributed by both year (2001, 2002) and plot between the blowdown and control plots. To mitigate issues of spatial dependence, we required all of the selected cells within the same year to be a minimum of 50 m apart, and we did not select the same cell in successive years. So that we could later perform a joint analysis using both bird and vegetation data, we further required that selected grid cells were those for which we had also collected vegetation data in the same year. After cell selection, we recorded by species (based upon our territory maps) the percentage of each selected cell covered by a territory. For summary purposes, species were assigned to foraging guilds (e.g., tree-foliage searcher, timber gleaner) according to those described by Bock and Lynch (1970). Next, we tested these data for homogeneity of variance (Levene's test) and used a one-way ANOVA to test for the effect of disturbance. Although somewhat unconventional, distinguishing bird use by measuring the percentage of each cell covered by a territory allowed us to detect differences between plots on a finer scale—an attribute we felt was required, given the patchiness of the landscape following the blowdown. We are aware that changes in both avian density (Huxley 1934, Wiens et al. 1985) and habitat (Gill and Wolf 1975, Smith and Shugart 1987) may affect territory size, but upon finding lit-

tle difference in average territory size between plot types (blowdown or control), we concluded that significant differences in territory cover per cell would likely be the result of more territories rather than territories of a larger size.

In examining the relationship between habitat structure and bird species composition, we used only the 42 grid cells (21 blowdown, 21 control) from 2001 and 2002 for which we had both vegetation and bird data. First, we used a Pearson correlation matrix along with principal components analysis (PCA) to minimize redundancy within the dataset, following the recommendations of ter Braak (1986, 1994) for subsequent canonical correspondence analysis (CCA). If  $\geq 2$  variables were strongly correlated ( $r > 0.60$ ) within the correlation matrix, we kept only the habitat variable most strongly correlated with the first principal component (i.e., the variable explaining a greater amount of the variation within the data). Next, using the remaining variables (10 of 19), we performed PCA again to reduce the complexity of the dataset and summarize the habitat variables within the blowdown and control areas. Finally, we conducted CCA, performed by the PC-ORD statistical package (McCune and Mefford 1999), on the 10 selected habitat variables and 15 common bird species (those with territory cover in at least 10% of the 42 grid cells) to investigate more closely the relationship between habitat characteristics and the distribution of bird species. To determine the significance level of this relationship (ter Braak 1987), the CCA included a Monte Carlo test on the first two canonical functions, conducted with 1,000 permutations and using time of day as the source for randomization. Means are presented  $\pm$  SE.

## RESULTS

Twenty-six percent (5 of 19) of the habitat variables examined in the blowdown were significantly different after the storm in 2001 or 2002 when compared with pre-storm estimates collected in 1996 (Table 1). In contrast, there were no significant differences in habitat variables between years (1998, 2001, 2002) in the control. Percent tree cover (CTREE), which was somewhat higher in the to-be disturbed area before the storm (control:  $40.1 \pm$

$4.38$ , blowdown:  $51.6 \pm 3.75$ ), was significantly greater in the control after the windstorm in both 2001 (control:  $42.9 \pm 5.47$ , blowdown:  $23.4 \pm 5.07$ ) and 2002 (control:  $37.6 \pm 6.08$ , blowdown:  $7.6 \pm 3.23$ ). A similar trend was observed in diameter of live trees (LIVDIA) in the blowdown area: mean diameter decreased by 2002 ( $7.9 \pm 0.86$ ) to only half that observed before the storm ( $15.6 \pm 1.49$ ). Whereas it was not significantly different before the storm, evergreen tree cover (CTREE) and shrub or tree cover (CVR) were also significantly greater in the control than in the blowdown after the disturbance. On the other hand, percent shrub cover (CSHRB) was significantly greater in the control before the blowdown (control:  $44.1 \pm 5.06$ , blowdown:  $22.6 \pm 2.04$ ), but was not significantly different afterwards in either 2001 (control:  $45.3 \pm 3.96$ , blowdown:  $46.5 \pm 5.15$ ) or 2002 (control:  $42.8 \pm 5.78$ , blowdown:  $32.2 \pm 3.45$ ) due to tipped trees and broken-topped trees that were still alive in both years. The volume of coarse woody debris (DEBRIS)—the only variable that was not measured before the storm—was greater ( $P < 0.001$ ) in the blowdown during both 2001 (control:  $57.3 \pm 12.35$ , blowdown:  $93.3 \pm 15.43$ ) and 2002 (control:  $33.6 \pm 8.78$ , blowdown:  $89.4 \pm 14.05$ ).

Of the 30 bird species with identified territories in either the blowdown or control, 18 had territories in both plot types. Two species had territories only in the control while nine species had territories exclusively in the blowdown. Seven territorial and visitor species recorded in the blowdown were not recorded in the control, whereas all species recorded in the control had territories or were recorded as visitors in the blowdown.

Species for which we detected a greater percentage of territory cover per grid cell in the blowdown included Black-and-white Warbler (scientific names listed in Table 2; control:  $2.1 \pm 1.49$ , blowdown:  $13.3 \pm 4.49$ ,  $F_{1,40} = 5.60$ ,  $P = 0.023$ ), Chestnut-sided Warbler (control: 0, blowdown:  $12.1 \pm 4.35$ ,  $F_{1,40} = 7.81$ ,  $P = 0.008$ ), and Mourning Warbler (control: 0, blowdown:  $16.2 \pm 5.72$ ,  $F_{1,40} = 8.01$ ,  $P = 0.007$ ; Table 2). Species with a greater percentage of territory cover per cell in the control included Blackburnian Warbler (control:  $20.5 \pm 6.57$ , blowdown:  $3.3 \pm 1.90$ ,

TABLE 2. Mean 2001 and 2002 percent bird territory cover per cell ( $\pm$ SE), bird frequency (number of cells with territory cover), and outcomes of one-way ANOVA between 21 blowdown and 21 control cells following a catastrophic 1999 blowdown in a black spruce–balsam fir forest in the Superior National Forest, Minnesota. Results are presented by foraging guild. Birds detected, but not considered territorial, were recorded as visitors (V).

Guild/Species	Micromenic	Control <sup>a</sup>	Blowdown	Frequency	$F_{1,40}$	P
<b>Flycatchers</b>						
Yellow-bellied Flycatcher ( <i>Empidonax flaviventris</i> )	YBFC	4.5 $\pm$ 2.95	18.8 $\pm$ 5.84	12	4.76	0.035
Alder Flycatcher ( <i>Empidonax althorum</i> )	ALFC	—	6.2 $\pm$ 4.17	4	2.21	0.15
Least Flycatcher ( <i>Empidonax minimus</i> )	LEFC	1.0 $\pm$ 0.95	6.4 $\pm$ 4.70	3	1.31	0.26
<b>Ground-brush foragers</b>						
Winter Wren ( <i>Troglodytes troglodytes</i> )	WIWR	4.6 $\pm$ 2.05	13.1 $\pm$ 5.36	14	2.18	0.15
Swainson's Thrush ( <i>Catharus ustulatus</i> )	SWTH	19.0 $\pm$ 6.25	12.4 $\pm$ 4.35	17	0.75	0.39
Hermit Thrush ( <i>Catharus guttatus</i> )	HETH	1.0 $\pm$ 0.95	3.8 $\pm$ 3.34	3	0.68	0.42
Nashville Warbler ( <i>Vermivora ruficapilla</i> )	NAWA	30.7 $\pm$ 7.68	17.6 $\pm$ 6.62	19	1.67	0.20
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )	CSWA	—	12.1 $\pm$ 4.35	8	7.81	0.008
Ovenbird ( <i>Seiurus aurocapilla</i> )	OVBI	—	1.9 $\pm$ 1.36	2	1.97	0.17
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	NOWT	—	1.4 $\pm$ 1.43	1	1.00	0.32
Mourning Warbler ( <i>Oporornis philadelphia</i> )	MOWA	V	16.2 $\pm$ 5.72	9	8.01	0.007
Chipping Sparrow ( <i>Spizella passerina</i> )	CHSP	6.8 $\pm$ 4.45	10.2 $\pm$ 5.57	7	0.23	0.63
Swamp Sparrow ( <i>Melospiza georgiana</i> )	SWSP	—	1.9 $\pm$ 1.91	1	1.00	0.32
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	WTSP	19.4 $\pm$ 6.19	33.6 $\pm$ 6.35	25	2.55	0.12
<b>Timber gleaners</b>						
Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	RBNH	7.0 $\pm$ 4.50	V	4	2.42	0.13
Brown Creeper ( <i>Certhia americana</i> )	BNCR	3.3 $\pm$ 2.52	1.9 $\pm$ 1.91	3	0.21	0.65
Black-and-white Warbler ( <i>Mniotilta varia</i> )	BWVA	2.1 $\pm$ 1.49	13.3 $\pm$ 4.49	10	5.60	0.023
<b>Tree-foliage searchers</b>						
Blue-headed Vireo ( <i>Vireo solitarius</i> )	BHVI	—	8.1 $\pm$ 4.85	3	2.79	0.10
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	REVI	2.1 $\pm$ 2.14	12.6 $\pm$ 4.23	8	4.87	0.033
Black-capped Chickadee ( <i>Parus atricapillus</i> )	BCCH	0.7 $\pm$ 0.71	V	1	1.00	0.32
Boreal Chickadee ( <i>Parus hudsonicus</i> )	BOCH	0.7 $\pm$ 0.71	1.4 $\pm$ 1.43	2	0.20	0.66
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	GCKI	16.2 $\pm$ 4.62	0.7 $\pm$ 7.14	13	11.03	0.002
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	RCKI	3.1 $\pm$ 2.45	1.9 $\pm$ 1.91	3	0.15	0.70
Tennessee Warbler ( <i>Vermivora peregrina</i> )	TEWA	3.3 $\pm$ 2.32	1.4 $\pm$ 1.43	3	0.49	0.49
Northern Parula ( <i>Parula americana</i> )	NOPA	2.7 $\pm$ 1.50	0.2 $\pm$ 0.24	5	2.66	0.11
Magnolia Warbler ( <i>Dendroica tigrina</i> )	MAWA	28.1 $\pm$ 5.78	31.0 $\pm$ 6.33	29	0.11	0.75
Cape May Warbler ( <i>Dendroica magna</i> )	CMWA	V	2.4 $\pm$ 1.78	2	1.79	0.19
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	YRWA	9.0 $\pm$ 3.41	1.0 $\pm$ 7.42	10	5.38	0.026
Blackburnian Warbler ( <i>Dendroica fusca</i> )	BKWA	20.5 $\pm$ 6.57	3.3 $\pm$ 1.90	11	6.28	0.016
Canada Warbler ( <i>Wilsonia canadensis</i> )	CAWA	—	10.5 $\pm$ 5.87	3	3.19	0.082

<sup>a</sup> Dashes indicate that the species was not recorded, either with a territory or as a visitor in the control.

TABLE 3. Selected habitat variables and associated correlations with each of three principal components having eigenvalues >1. PCA based on 2001 and 2002 data from 21 blowdown and 21 control cells, Superior National Forest, Minnesota.

Habitat variable	PC 1	PC 2	PC 3
% tree cover	0.43	-0.08	-0.08
No. dead trees/ha	0.17	-0.33	-0.54
Live tree diameter (cm)	0.40	-0.10	0.34
% shrub cover	0.35	-0.12	-0.06
No. live shrub stems/ha	0.32	0.53	0.00
No. dead shrub stems/ha	0.35	0.01	-0.18
% herb cover	0.17	-0.46	-0.06
% bryophyte cover	0.31	-0.14	-0.16
% coarse litter cover	0.18	-0.31	0.72
Coarse woody debris (m <sup>3</sup> /ha)	-0.34	-0.51	-0.02

$F_{1,40} = 6.28$ ,  $P = 0.016$ ). Golden-crowned Kinglet (control:  $16.2 \pm 4.62$ , blowdown:  $0.7 \pm 7.14$ ,  $F_{1,40} = 11.03$ ,  $P = 0.002$ ) and Yellow-rumped Warbler (control:  $9.0 \pm 3.41$ , blowdown:  $1.0 \pm 7.42$ ,  $F_{1,40} = 5.38$ ,  $P = 0.026$ ; Table 2).

By foraging guild, 6 of the 14 (43%) species of ground-brush foragers and flycatchers held territories in the blowdown but not in the control; 6 of the 8 (75%) species holding territories in both blowdown and control had a greater percentage of territory cover in the blowdown than in the controls. Four of the 13 (31%) species of tree-foliage searchers had more territory cover in the control (all  $P < 0.05$ ). Only the Red-eyed Vireo had a greater percentage of territory cover in the blowdown (control:  $2.1 \pm 2.14$ , blowdown:  $12.6 \pm 4.23$ ,  $F_{1,40} = 4.87$ ,  $P = 0.033$ ; Table 2).

Three principal components had eigenvalues >1 (PC 1 = 3.71, PC 2 = 1.78, PC 3 = 1.18) and together explained 67% of the variance in the vegetation dataset. The first principal component explained 37% of the variance and was positively correlated with the diameter of live trees and tree cover, while being negatively correlated with the volume of debris (Table 3). The second component, which explained 18% of the variance, was positively correlated with the number of live shrub stems and negatively correlated with the volume of debris (Table 3). A plot of PC 1 versus PC 2 (not shown) revealed only slight overlap of blowdown and control cells, indicating that the 10 habitat variables retained for use with the CCA reasonably separate one type from the other.

The Monte Carlo permutations test conducted with the CCA indicated that both the first canonical function ( $P = 0.027$ ) and the overall test ( $P = 0.010$ ) were significant, with the correlation between selected species and habitat being relatively high ( $r = 0.84$ ). The first axis of the CCA accounted for 9.9% of the variation in the bird data, and was positively correlated with the volume of debris (DEBRIS,  $r = 0.51$ ) and negatively correlated with tree cover (CTREE,  $r = -0.72$ ). Bird species preferring heavy cover at or near the ground with little to no canopy cover (Mourning Warbler, Chestnut-sided Warbler, Yellow-bellied Flycatcher, and Winter Wren) were positively correlated with the first axis—the volume of debris in particular—and are shown in the extreme right hand portion of Figure 2. Species such as the Golden-Crowned Kinglet, Blackburnian Warbler, Swainson's Thrush, and Northern Parula were negatively correlated with the first axis and preferred more tree cover (Fig. 2).

Although not significant, the second canonical function explained 5.0% of the variance in the bird data (Monte Carlo test:  $P = 0.21$ ) and was positively correlated with bryophyte cover (CBRYO,  $r = 0.66$ ) and herb cover (CHERB,  $r = 0.41$ ). Birds most closely associated with bryophyte and herb cover included Nashville Warbler, Northern Parula, and White-throated Sparrow.

## DISCUSSION

Our data suggest that the primary effect of the 4 July 1999 storm was a significant decrease in tree canopy and the diameter of live

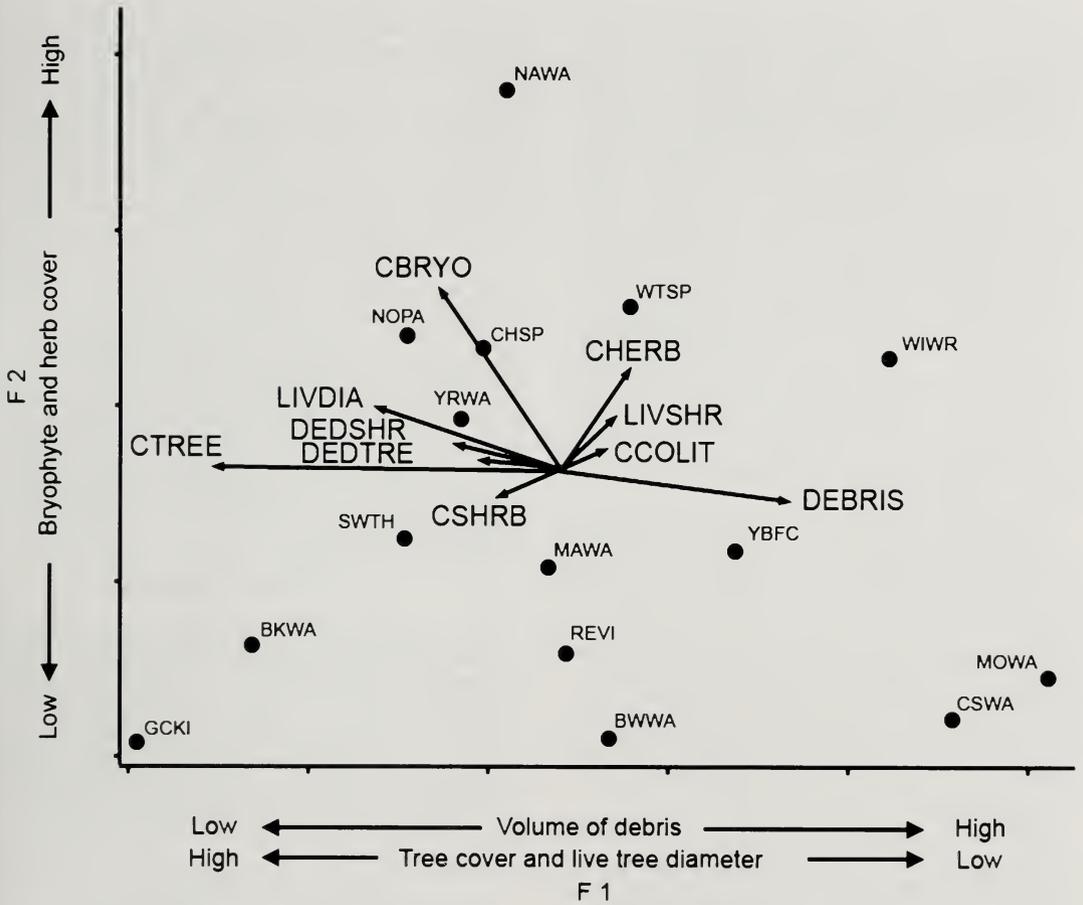


FIG. 2. Bird distribution and vegetation variables (2001, 2002 data) based on functions 1 (F1) and 2 (F2) of a canonical correspondence analysis of 10 vegetation variables (codes defined in Table 1) and 15 bird species (codes defined in Table 2) from 21 blowdown cells and 21 control cells following a catastrophic 1999 blowdown in a black spruce–balsam fir forest in the Superior National Forest, Minnesota. The length and direction of the vector for each habitat variable corresponds to the level of its correlation with each function.

trees, with a concomitant increase in shrub layer structure and coarse woody debris. Tree cover, which was generally characterized by black spruce, balsam fir, and paper birch (*Betula papyrifera*), was slightly greater in the pre-blowdown but reduced to half that of the control as a result of the windstorm. The wind also decreased the number of live trees and the diameter of both live and dead trees by blowing over or breaking off all but the largest dead trees and most of the bigger live trees. In the shrub layer, fallen trees and tree-tops eliminated disparities between disturbance and control plots with respect to shrub cover and the number of live shrub stems that existed before the storm by increasing the

amount of cover at or near the ground in the blowdown area. Coarse woody debris in the blowdown area also increased significantly as a result of the storm.

Many researchers have documented the importance of coarse woody debris to avian communities (Davis et al. 1999, Greenberg and Lanham 2001, Lohr et al. 2002), citing increases in nest-site suitability and food availability as possible explanations (Lohr et al. 2002) for its importance. Chestnut-sided and Mourning warblers, which were strongly associated with the volume of coarse woody debris, are often associated with dense shrubbery and open woods of early successional forests (Apfelbaum and Haney 1981, Ehrlich

et al. 1988, Schulte and Niemi 1998). Winter Wren was also associated with the low-canopy blowdown despite being typically associated with old-growth forests (Hejl et al. 2002). Yellow-bellied Flycatcher, White-throated Sparrow, and Black-and-white Warbler also showed some preference for areas with higher levels of coarse woody debris, with all but the White-throated Sparrow having significantly more territory cover in the blowdown. Red-eyed Vireo, a species often associated with closed-canopy or mature forest (James 1976, Faanes and Andrew 1983), also had significantly more territory cover in the blowdown but has been shown to respond better than expected to canopy loss (Greenberg and Lanham 2001, Faccio 2003).

Golden-crowned Kinglet and Blackburnian Warbler had significantly more territory cover in the control than in the blowdown and were highly correlated with the overall amount of tree canopy cover and the diameter of live trees (Fig. 2). Both species typically forage, and spend most of their time, high in the trees (Ehrlich et al. 1988, Morse 1994), and their numbers would likely decline if that stratum were reduced.

Overall, a significant decrease in tree canopy cover and the volume of coarse woody debris have provided more opportunities for species that forage or nest (or both) at or near the ground, while limiting opportunities for species more likely to use tree canopies. While these effects do parallel some of the responses to fire or timber-harvest disturbances, differences are apparent as well. Both wind and fire lead to a decline in tree canopy, greater numbers of snags, and an increase in ground and shrub-layer cover. After fire, however, trees often die slowly over several years, and, in the Great Lakes region, they may remain standing for several years before contributing to the volume of coarse woody debris. In contrast, severe wind resulted in an immediate decrease in tree cover and a corresponding increase in shrub-layer structure and coarse woody debris. Like the effects of wind, logging activities also result in a reduction of tree canopy and tree stem density, and an increase in coarse woody debris.

Similar to what we found after the wind-storm, post-fire bird communities are typically distinguished by higher densities of flycatch-

ers and ground-brush foragers and fewer tree-foliage searchers (Apfelbaum and Haney 1986, Drapeau et al. 2000, Morissette et al. 2002). The effect of logging on bird communities is largely dependent upon the number of residual trees and snags and the amount of coarse woody debris (Brawn et al. 2001, Lohr et al. 2002). Unlike fire or wind, relatively few snags remain after clear-cuts, which leads to a nearly complete change in avian community composition (Schieck and Hobson 2000, Brawn et al. 2001). Natural disturbances like wind, and arguably timber harvests in some cases, result in more heterogeneous landscapes as a result of different seral stages (Niemi et al. 1998), thereby enhancing the diversity of bird communities (Angelstam 1998, Brawn et al. 2001).

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## USE OF GROUP-SELECTION AND SEED-TREE CUTS BY THREE EARLY-SUCCESSIONAL MIGRATORY SPECIES IN ARKANSAS

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**ABSTRACT.**—Silviculture in the Ouachita National Forest in Arkansas and Oklahoma has shifted in recent years from mostly even-aged management to a mix of even- and uneven-aged regeneration systems, including group-selection. Researchers have described presence/absence of early-successional bird species in forest openings created by even- and uneven-aged silviculture, but few have examined nest success. We examined occupancy and nest success of three early-successional species—Indigo Bunting (*Passerina cyanea*), Yellow-breasted Chat (*Icteria virens*), and Prairie Warbler (*Dendroica discolor*)—within 6- and 7-year-old openings created by group-selection (uneven-aged,  $\leq 0.8$  ha) and seed-tree (even-aged, 11–16 ha) cuts in Arkansas. We found 54 Indigo Bunting nests in openings created by seed-tree cuts and 28 in openings created by group-selection cuts (hereafter “seed-tree stands” and “group-selection stands,” respectively). We found 50 Yellow-breasted Chat nests in seed-tree stands, but only 2 were found in group-selection stands. We found 14 Prairie Warbler nests in seed-tree and none in group-selection stands. Mayfield nest success for Indigo Bunting was 30.9% in seed-tree stands and 41.9% in group-selection openings, but there was no difference in daily nest survival ( $0.952 \pm 0.009$  and  $0.964 \pm 0.010$ , respectively;  $\chi^2 = 0.792$ ,  $P = 0.37$ ). Our data suggest that Indigo Buntings can nest successfully in both regenerating seed-tree and group-selection stands; however, group-selection openings may be too small to support nesting Yellow-breasted Chats and Prairie Warblers. Public concerns about clear-cutting have resulted in increased use of uneven-aged management by the USDA Forest Service. However, before widespread implementation of group-selection cutting, additional research should be conducted to evaluate the effects of this management strategy on Neotropical migratory bird communities. Received 18 November 2004, accepted 24 August 2005.

Due to growing public concerns about clear-cutting and planting, the USDA Forest Service (USFS) is now relying more on natural regeneration systems involving both even-aged (e.g., seed-tree and shelterwood) and uneven-aged (e.g., single-tree and group-selection) silvicultural practices (Thill and Koerth 2005). On the Ouachita National Forest (ONF) in west-central Arkansas and east-central Oklahoma, clear-cutting has been largely replaced by seed-tree, shelterwood, single-tree, and group-selection management. Seed-tree management is similar to clear-cutting, but relies on natural regeneration from trees (typically 10–25 mature trees/ha) that are retained as a seed source (Holland et al. 1990). Under group-selection management, roughly 10% of the stand is clear-cut every 10

years within small ( $\leq 0.8$  ha) patches that are allowed to regenerate naturally. If the surrounding stand (matrix) contains sufficient timber volume, it also may be thinned concurrently with the patch cuts (Smith 1986, Baker et al. 1996). Following a succession of treatments, this system creates a mosaic of forest patches of differing seral stages.

In general, tree removal results in the decline of many forest-interior bird species (Robinson et al. 1995, Thompson et al. 1995, Annand and Thompson 1997). Clear-cutting and heavy thinning treatments, however, can create habitat for a suite of early-successional bird species that would otherwise not occur, or occur infrequently, in forested landscapes (Annand and Thompson 1997, Germaine et al. 1997, Costello et al. 2000). Many of these early-successional species have experienced widespread population declines in recent years (Askins 1993, Litvaitis 1993). Group-selection silviculture may be appealing to wildlife managers because it creates habitat for early-successional species and allows some species that require mature forest to remain in the forest matrix after harvest (Chambers et al. 1999, Robinson and Robinson 1999, Costello et al. 2000). Furthermore, group-selection silvicult-

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ture may increase overall bird abundance and diversity in some areas relative to untreated stands (Germaine et al. 1997). However, recent studies have shown that some early-successional species that occur in large forest openings do not use, or occur less frequently, in the smaller openings created by group-selection cuts (Annand and Thompson 1997, Rodewald and Smith 1998, Robinson and Robinson 1999, Costello et al. 2000). These data suggest that group-selection silviculture may not be suitable for some early-successional bird species in forested landscapes, and that a mix of silvicultural techniques may be necessary to maintain populations of these species (Annand and Thompson 1997, Chambers et al. 1999, Costello et al. 2000).

Whereas species presence/absence data are meaningful, they are not sufficient to uncover causes of reproductive failure that may limit populations associated with different silvicultural practices (Donovan et al. 1995). Several recent studies were designed to evaluate nest success in stands treated with group-selection harvests (e.g., King et al. 2001, Twedt et al. 2001, Gram et al. 2003, King and Degraaf 2004); however, only a few compared nest success of early-successional species in regenerating group-selection cuts to that in other treatments (King et al. 2001, Gram et al. 2003). Barber et al. (2001) compared nesting success on the ONF under several silvicultural treatments, including single-tree selection, but there are no data for evaluating nesting success under group-selection systems in this area. These data are needed, however, because the ONF plans substantial use of group-selection silviculture in the future.

Our objective was to compare occupancy and nesting success of three early-successional Neotropical migrants within stands treated with traditionally sized ( $\leq 0.8$  ha) group-selection cuts and larger seed-tree cuts (10–16 ha) in the Ouachita Mountains of Arkansas. We chose the latter treatment because it is one of the primary even-aged regeneration systems being used on the ONF. We predicted that nest success would be lower in the small, group-selection cuts than in the larger seed-tree cuts. We also predicted higher rates of nest predation in group-selection than in seed-tree cuts. Parasitism by Brown-headed Cowbirds (*Molothrus ater*) is low on the ONF (Barber et al.

2001) and elsewhere in forested landscapes (Hoover and Brittingham 1993, Hoover et al. 1995, Hanski et al. 1996); therefore, we did not expect parasitism to be an important cause of nest failure. In addition to examining occupancy and nest success, we also evaluated microhabitat characteristics at nest sites. We compared habitat structure (1) between nests in small openings created by group-selection silviculture and those in larger openings created by seed-tree silviculture, and (2) between successful and unsuccessful nests.

## METHODS

*Study area.*—Our study was conducted in 2000 and 2001 on the easternmost portion of the ONF in Garland, Perry, and Saline counties, Arkansas. Mixed pine-hardwood stands on the ONF occur at elevations ranging from approximately 90 to 820 m, and are characterized by a diverse mix of vegetation dominated by shortleaf pine (*Pinus echinata*), oaks (*Quercus* spp.), and hickories (*Carya* spp.). Common hardwoods include white oak (*Quercus alba*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), mockernut hickory (*Carya tomentosa*), red maple (*Acer rubrum*), black tupelo (*Nyssa sylvatica*), winged elm (*Ulmus alata*), and flowering dogwood (*Cornus florida*). Common shrubs include winged sumac (*Rhus copallinum*), bigleaf snowbell (*Styrax grandifolia*), American beautyberry (*Callicarpa americana*), sparkleberry (*Vaccinium arboreum*), and other *Vaccinium* species.

Our study areas included three group-selection and three seed-tree stands; one of the latter had to be replaced in 2001 because it was inadvertently burned after the 2000 field season. Each treatment was 6 years post-harvest at the initiation of this study in 2000. Seed-tree stands ranged from 11 to 16 ha in size. Two of the group-selection stands were 12 ha, and each contained three openings. The third group-selection stand was 36 ha, and contained 15 openings. Our group-selection stands had been subjected only to their first treatment in a series of harvests; thus, these stands were in transition from an even-aged to an uneven-aged condition. The 21 group-selection openings from our three stands ranged in size from 0.14 to 0.76 ha (mean =

0.33 ha); however, 19 (91%) of the openings were  $<0.40$  ha, which is half the upper limit (0.8 ha) used under traditional group-selection management. The mean nearest-neighbor distances between adjacent group-openings in the two smaller stands were 169 and 131 m, and the mean in the larger stand was 48 m. The ratios of early successional to forested habitat in the smaller group-selection stands were 1.0:13.8 and 1.0:7.5 ha, and the ratio in the larger stand was 1.0:9.0 ha.

**Fieldwork.**—Fieldwork was conducted between early May and mid-August in 2000 and 2001. We chose three focal study species—Indigo Bunting (*Passerina cyanea*), Yellow-breasted Chat (*Icteria virens*), and Prairie Warbler (*Dendroica discolor*)—for monitoring nest success in regenerating seed-tree and group-selection stands. These species were selected because they are common in forest openings in the ONF and their nests are relatively easy to find.

We located nests of target species by following adults carrying nest material or food, by observing them return to their nests to resume incubation, and by systematic searches of the study areas. We found a few additional Yellow-breasted Chat nests by attaching radio transmitters (Johnson et al. 1991) to the backs of females that we caught with mist nets. We tracked these birds until we found their nests or until the transmitters fell off. Nests were monitored an average of once every 3–4 days following the techniques of Martin and Geupel (1993). Whenever possible, we used binoculars to check nest status from a distance; however, we approached nests and checked contents when we expected a transition from one nesting phase to the next (e.g., incubation to nestling). When checking nest contents, we approached from one path and left from another to reduce the probability of attracting predators. Nests were considered successful if at least one host young fledged from the nest. Fledging was confirmed if we observed fledglings, heard begging calls outside of the nest, or observed adults carrying food or behaving defensively (chipping) on or near the expected fledging date. Nests were considered depredated if they were empty prior to the expected fledging date.

Habitat characteristics of nest sites were quantified within 5.0- and 11.3-m-radius cir-

cles (0.04 ha) centered on the nests, following a modified BBIRD Protocol (Martin et al. 1997). Between late June and August of each year, we measured habitat characteristics after nests had failed or the young had fledged. We did not conduct habitat sampling at nests that were abandoned prior to egg laying, deserted with eggs or chicks in the nest, or when nest fate was unknown.

Characteristics measured at nests included nest height, height and diameter of the nest plant, number and mean diameter of branches supporting the nest, and distance from the nest to the nearest forest edge. We also visually estimated nest concealment (from 1 m away) from the side of the nest in each of the four cardinal directions. At each location, we assigned a concealment index value from 1 to 6 (1 = 0–5, 2 = 6–25, 3 = 26–50, 4 = 51–75, 5 = 76–95, and 6 = 96–100%), corresponding to the percent of the nest that was concealed by vegetation. We then calculated the mean index value for concealment from the side.

Habitat characteristics measured within the 5.0-m-radius circles included slope, mean shrub height, shrub density in two size classes ( $\leq 2.5$  and  $>2.5$ –8.0 cm diameter), and indices of various types of ground cover, including shrubs (in three height classes: 0–0.5, 0.5–1, and  $>1$  m), grasses, forbs, ferns, vines, leaf litter, downed logs, and bare ground. Slope of the circle was measured using a clinometer. For all other measurements, we divided the circle into four quadrants, bounded by the four cardinal directions (Martin et al. 1997). Each characteristic was measured within each of the four quadrants, and a mean value was calculated. Mean shrub height was estimated visually using a meter stick as a reference. We considered all trees  $<3$  m in height to be shrubs. We calculated shrub density by counting the number of stems in each size class within a 1-m<sup>2</sup> quadrat placed in each of the four quadrants of the circle. Indices of ground cover were estimated visually using the same categories as those used for nest concealment.

Characteristics measured in the 11.3-m-radius circles included mean tree height, percent canopy cover, and density of trees and snags. We used a clinometer to measure the height of all trees in the circle, and then calculated the mean height. Canopy cover was measured using a concave spherical densiometer. For

tree and snag density, we separated trees into three size classes (8–23, >23–38, and >38 cm dbh) and snags into two size classes ( $\leq 12$  and  $> 12$  cm dbh). Density was calculated by counting the number of trees and snags in each size class.

*Statistical analyses.*—We calculated daily nest survival probabilities for Indigo Bunting and Yellow-breasted Chat using the Mayfield (1975) method with the standard error estimator developed by Johnson (1979). We did not use the Mayfield method for Prairie Warbler because we found too few ( $< 20$ ) nests (Hensler and Nichols 1981); instead, we calculated apparent nest success (the number of successful nests divided by the total number of nests). For Indigo Bunting and Yellow-breasted Chat, we calculated daily survival probabilities for each phase of nesting (egg laying, incubation, and nestling), as well as for the entire nesting period. We only included nests in the Mayfield analysis that were observed for  $> 1$  day (i.e., we did not include nests that were found on the day of failure or fledging). Survival estimates were based on a 25-day nesting period for Indigo Bunting (4 egg-laying days, 12 incubation days, and 9 nestling days) and a 24-day nesting period for Yellow-breasted Chat (4 egg-laying days, 12 incubation days, and 8 nestling days) based on our nest-monitoring data. To calculate nest success, survival probabilities were raised to the power of the number of days in the nesting period (e.g., daily nest survival<sup>25</sup> = nest success for Indigo Bunting). We tested for a year effect between 2000 and 2001 by comparing daily nest survival of Indigo Bunting and Yellow-breasted Chat using program CONTRAST (Hines and Sauer 1989) and an alpha level of 0.05. There were no significant differences between years for either species; therefore, we used CONTRAST (Hines and Sauer 1989) to compare daily nest survival of Indigo Bunting in seed-tree versus group-selection stands. We did not compare daily survival between the two stand types for Yellow-breasted Chat because we found too few nests in group-selection stands. We could not compare apparent nest success of Prairie Warbler in the two stand types because this species did not nest in group-selection stands.

We used Minitab (Minitab, Inc. 1998) to conduct all statistical analyses for habitat var-

iables. We examined plots of the data and tested for normality. Most habitat variables were normally distributed; therefore, we tested for a year effect using two-sample *t*-tests (alpha level = 0.05). Nest-site habitat characteristics were similar between years for all species and data were pooled across years. We used two-sample *t*-tests to compare nest-site habitat variables between group-selection and seed-tree stands for Indigo Bunting. To determine whether habitat variables differed between the two stand types, we also evaluated effect size and 95% CI around the effect size (Anderson et al. 2001, Di Stefano 2004) instead of using only the *P*-values generated from *t*-tests.

To determine which habitat variables best explained nest success, we conducted binary logistic regression analysis. Logistic regression was conducted for Indigo Bunting nests in group-selection and seed-tree stands as well as for all nests pooled, and for Yellow-breasted Chat nests in seed-tree stands. Successful and unsuccessful nests were binary independent variables. For each analysis, we reduced the number of candidate independent variables by conducting univariate logistic regression analyses for each habitat variable (Hosmer and Lemeshow 1989)—retaining variables that differed between successful and failed nests and using an alpha level of  $\leq 0.15$ . We tested for correlation between the retained variables by calculating Pearson correlation coefficients; when two or more variables were correlated ( $P < 0.05$ ), we included the variable that we thought was more biologically meaningful, based on our knowledge of the birds' behavior and ecology. For each analysis, we then performed logistic regression using all variables (full model) and on all subsets of the full model. We ranked models using Akaike's Information Criterion modified for small sample size ( $AIC_c$ ; Anderson et al. 2001), and present all models where  $\Delta AIC_c < 2$ . If  $\Delta AIC_c$  for all other candidate models was  $> 2$ , we present the second-best model as a comparison. Model fit was evaluated using the Hosmer-Lemeshow lack-of-fit test (Hosmer and Lemeshow 1989), in which higher *P*-values indicate that the data fit the model well.

## RESULTS

*Nest success.*—We found a total of 82 Indigo Bunting (54 in seed-tree and 28 in group-

TABLE 1. Daily survival for Indigo Bunting nests in seed-tree ( $n = 48$ ) and group-selection stands ( $n = 25$ ) on the Ouachita National Forest, Arkansas, 2000–2001.

Nest phase	Seed-tree			Group-selection			$\chi^2$	$P^a$
	Failed nests	Exposure days	Daily survival $\pm$ SE	Failed nests	Exposure days	Daily survival $\pm$ SE		
Egg laying	1	21	0.952 $\pm$ 0.047	1	26	0.962 $\pm$ 0.038	0.231	0.88
Incubation	8	283	0.972 $\pm$ 0.010	6	195	0.969 $\pm$ 0.012	0.248	0.88
Nestling	17	242	0.930 $\pm$ 0.017	5	117	0.957 $\pm$ 0.019	1.209	0.27
Total	26	545	0.952 $\pm$ 0.009	12	338	0.964 $\pm$ 0.010	0.792	0.37

<sup>a</sup>  $\chi^2$  and  $P$ -values were calculated using program CONTRAST (Hines and Sauer 1989).

selection stands), 52 Yellow-breasted Chat (50 in seed-tree and 2 in group-selection stands), and 14 Prairie Warbler (all in seed-tree stands) nests. The two chat nests in group-selection stands were found during different years, but both were located in the same stand and within the largest of all 21 group-openings (0.76 ha). We observed male Prairie Warblers in 3 of the 21 group-selection openings, but we did not observe any females or nesting activity at these sites. As these two latter species were rarely found in group-selection stands, we could not compare nesting success between the two treatment types.

Mayfield nest success for Yellow-breasted Chats in seed-tree stands was 31.3% ( $n = 46$  nests, excluding 4 discovered on the day of fledging or failure) and overall daily nest survival was  $0.951 \pm 0.009$  SE. Both chat nests found in group-selection stands failed. Apparent nest success for Prairie Warblers was 45.4% ( $n = 11$ ). Three Prairie Warbler nests were not included because we could not determine nest fate.

Mayfield nest success for Indigo Buntings was 41.0% in group-selection ( $n = 25$ ) and 29.2% in seed-tree stands ( $n = 48$ ), but there was no significant difference in daily nest survival between the two stand types (Table 1). Nine of the 82 nests were not included in the analysis because they were discovered either on the day of fledging or failure.

Predation was the primary cause of nest failure for Indigo Bunting (37 of 44 failed nests; 84.1%), Yellow-breasted Chat (30 of 33 failed nests; 90.9%), and Prairie Warbler (5 of 6 failed nests; 83.3%). For all species combined, 72 of 83 (86.7%) nests failed because of predation. Nest desertion (eggs or chicks present) was the second highest cause of nest failure for buntings (6 of 44 failed nests;

13.6%), chats (2 of 33 failed nests; 6.1%), and warblers (1 of 6 failed nests; 16.7%). Other causes of nest failure included nest abandonment prior to egg laying (1 of 33 failed nests; 3.0% for chats) and brood parasitism by Brown-headed Cowbird (1 of 44 failed nests; 2.3% for buntings). Overall nest predation for Indigo Bunting was 45.1% (37 of 82 nests). Cowbird eggs were observed in three bunting nests, but only one of these nests failed to fledge host young. The other two nests fledged at least one cowbird and one bunting. Overall nest predation for Yellow-breasted Chat was 57.7% (30 of 52 nests). Cowbird eggs were also observed in two chat nests (3.8%), but these nests failed due to predation. Overall nest predation for Prairie Warbler was 35.7% (5 of 14 nests). Cowbird parasitism was not observed in Prairie Warbler nests.

*Habitat characteristics.*—Eleven habitat variables differed between Indigo Bunting nests in seed-tree compared with group-selection stands (Table 2). Distance to forest edge, tree height, and grass and forb cover were greater at nests in seed-tree stands. Fern and vine cover, total tree density, density of trees 8–23 and >38 cm dbh, total snag density, and density of snags >12 cm dbh all were greater at nests in group-selection stands.

Based on the results of the univariate regressions and Pearson correlation tests, we identified four habitat variables for multiple logistic regression analysis that explained the variation in Indigo Bunting nest success in group-selection stands: diameter of branches supporting the nest, distance to forest edge, mean shrub height, and vine cover. The best models ( $\Delta AIC_c < 2$ ) explaining nest success in group-selection stands indicated that nests in areas with increased cover of vines were more likely to be successful (Table 3). The

TABLE 2. Habitat characteristics at Indigo Bunting nests in group-selection ( $n = 26$ )<sup>a</sup> and seed-tree ( $n = 42$ )<sup>a</sup> stands on the Ouachita National Forest, Arkansas, 2000–2001.

Habitat characteristic <sup>b</sup>	Group-selection mean $\pm$ SE	Seed-tree mean $\pm$ SE	Effect size	95% CI	$P^c$
Distance to forest edge (m)	15.80 $\pm$ 2.30	35.71 $\pm$ 6.88	-19.91	-5.27 to -34.56	0.009
Grass cover index <sup>d</sup>	1.86 $\pm$ 0.14	2.63 $\pm$ 0.15	-0.78	-0.36 to -1.19	<0.001
Forb cover index <sup>d</sup>	1.13 $\pm$ 0.03	1.55 $\pm$ 0.06	-0.42	-0.27 to -0.57	<0.001
Fern cover index <sup>d</sup>	1.42 $\pm$ 0.10	1.02 $\pm$ 0.01	0.40	0.20 to 0.60	<0.001
Vine cover index <sup>d</sup>	2.13 $\pm$ 0.16	1.71 $\pm$ 0.10	0.42	0.04 to 0.80	0.030
Tree height (m)	13.03 $\pm$ 0.68	17.55 $\pm$ 0.93	-4.52	-2.23 to -6.83	<0.001
Total tree density <sup>e</sup>	11.63 $\pm$ 1.80	6.12 $\pm$ 0.64	5.51	1.61 to 9.40	0.007
Tree density (8–23 cm dbh) <sup>e</sup>	8.48 $\pm$ 1.60	2.98 $\pm$ 0.54	5.51	1.98 to 9.03	0.003
Tree density (>38 cm dbh) <sup>e</sup>	0.93 $\pm$ 0.20	0.45 $\pm$ 0.12	0.47	0.00 to 0.95	0.049
Total snag density <sup>e</sup>	3.30 $\pm$ 0.49	1.00 $\pm$ 0.24	2.30	1.19 to 3.41	<0.001
Snag density (>12 cm dbh) <sup>e</sup>	2.37 $\pm$ 0.38	0.55 $\pm$ 0.17	1.82	0.98 to 2.66	<0.001

<sup>a</sup> Habitat characteristics were not measured at nests that were abandoned prior to egg laying, deserted with eggs or chicks in the nest, or when nest fate was unknown.

<sup>b</sup> See Alterman (2002) for nonsignificant habitat data.

<sup>c</sup>  $P$ -values from two-sample  $t$ -tests.

<sup>d</sup> Index based on cover classes described in methods.

<sup>e</sup> Tree and snag densities are reported per 0.04 ha.

best model also indicated that nests in areas with shorter shrubs were more likely to be successful. Four habitat variables were considered for multiple logistic regression models explaining variation in bunting nest success in seed-tree stands: nest height, nest concealment from the side, shrub cover 0.5–1.0 m, and mean tree height. The models that best explained variation in nests success in seed-tree stands ( $\Delta AIC_c < 2$ ) indicated that nests lower to the ground in areas with shorter trees were more likely to be successful (Table 3). The best model also indicated that nests in areas with increased cover of shrubs 0.5–1.0 m tall were more likely to be successful; however, the Hosmer-Lemeshow lack-of-fit test indicated that the data were not a good fit to the model (Table 3). Four habitat variables were also considered for multiple logistic regression models explaining variation in nest success for pooled Indigo Bunting nests: mean shrub height, vine cover, mean tree height, and density of trees >38 cm dbh. The model that best explained variation in nest success for the pooled sample indicated that nests in areas with shorter shrubs, shorter trees, and fewer large trees were more likely to be successful (Table 3). Increased vine cover was also an indicator of nest success in the second-best model.

Based on the results of the univariate regressions and Pearson correlation tests, we identified five habitat variables for inclusion

in multiple logistic regression analysis explaining variation in Yellow-breasted Chat nest success in seed-tree stands: nest height, nest concealment from the side, distance to forest edge, density of trees >38 cm dbh, and density of snags <12 cm dbh. Most of the models that best explained variation in nest success indicated that nests lower to the ground and farther from the forest edge were more likely to be successful (Table 3). Some of the models also indicated that nests in areas with fewer large trees and small snags were more likely to be successful.

## DISCUSSION

*Occupancy and nest success.*—Our data clearly show that Indigo Buntings can nest successfully in regenerating forest created by group-selection and seed-tree silviculture. Furthermore, daily nest survival was similar among treatments and we did not observe elevated levels of predation in group-selection openings. As expected, parasitism by Brown-headed Cowbird was very low for all species. Few studies have presented similar comparative data on nest success of early-successional species in large and small forest openings. Our results are consistent with those of King et al. (2001), who found no difference in daily nest survival for Chestnut-sided Warbler (*Dendroica pensylvanica*) in 6- to 10-ha clearcuts (0.993) and 0.2- to 0.7-ha group-selection cuts (0.987) in New Hampshire. They also

TABLE 3. Logistic regression models explaining nest success for Indigo Buntings and Yellow-breasted Chats on the Ouachita National Forest, Arkansas 2000–2001.

Species/Treatment	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	-2log(L)	w <sup>a</sup>	P <sup>b</sup>	Fit <sup>c</sup>
<b>Indigo Bunting</b>							
Group-selection stands	-3.148 + (-1.807 shrub height) + (2.922 vine cover) -1.466 + (-7.127 branch diameter) + (2.393 vine cover)	23.62	0.00	16.36	0.355	<0.001	0.269
Seed-tree stands	1.649 + (-2.773 nest height) + (2.294 shrub cover 0.5–1.0 m) + (-0.159 tree height)	48.96	0.00	38.74	0.264	0.006	0.016
Pooled	4.941 + (-2.261 nest height) + (-0.138 tree height)	49.57	0.61	42.31	0.195	0.011	0.174
	2.755 + (-1.338 shrub height) + (1.125 vine cover) + (-0.132 tree height) + (-0.737 tree density >38 cm dbh)	84.55	0.00	71.02	0.530	<0.001	0.209
	0.747 + (-1.142 shrub height) + (0.906 vine cover) + (-0.754 tree density >38 cm dbh)	87.51	2.95	77.29	0.120	0.001	0.356
<b>Yellow-breasted Chat</b>							
Seed-tree stands	2.028 + (-2.549 nest height) + (0.022 distance to edge) + (-0.647 tree density >38 cm dbh)	49.33	0.00	40.04	0.10	0.021	0.351
	1.100 + (-2.327 nest height) + (0.021 distance to edge)	49.57	0.24	42.82	0.09	0.031	0.689
	1.602 + (-2.413 nest height) + (0.018 distance to edge) + (-1.179 snag density <12 cm dbh)	50.00	0.67	40.71	0.07	0.028	0.863
	2.615 + (-2.752 nest height) + (0.020 distance to edge) + (-0.660 tree density >38 cm dbh) + (-1.273 snag density <12 cm dbh)	50.09	0.76	38.09	0.07	0.020	0.055
	2.275 + (-2.121 nest height) + (-1.300 snag density <12 cm dbh)	50.23	0.90	43.48	0.06	0.042	0.394
	3.270 + (-2.400 nest height) + (-0.613 tree density >38 cm dbh) + (-1.431 snag density <12 cm dbh)	50.44	1.11	41.15	0.06	0.034	0.087
	-0.467 + (0.022 distance to edge) + (-0.601 tree density >38 cm dbh)	50.55	1.22	43.80	0.05	0.050	0.551
	-1.079 + (0.020 distance to edge)	50.72	1.39	46.35	0.05	0.064	0.157
	-2.773 + (-2.208 nest height) + (-0.607 tree density >38 cm dbh)	50.73	1.40	43.98	0.05	0.055	0.612
	-0.704 + (0.017 distance to edge) + (-0.992 snag density <12 cm dbh)	51.04	1.71	44.29	0.04	0.064	0.106

<sup>a</sup> Akaike weight.  
<sup>b</sup> Probability values from  $\chi^2$  test indicating overall model significance.  
<sup>c</sup> Probability from Hosmer-Lemeshow lack-of-fit test (Hosmer and Lemeshow 1989).

found no difference in daily nest survival after pooling data for 16 species. Gram et al. (2003) also reported no difference in daily nest survival for Indigo Buntings in regenerating 3- to 13-ha clear-cuts (0.969) and stands treated with both group- and single-tree harvest (0.967) in the Missouri Ozarks.

From our study, it is evident that group-selection openings <0.4 ha may be too small to support nesting Yellow-breasted Chats or Prairie Warblers. This conclusion is consistent with Annand and Thompson's (1997) presence/absence data for these species in clear-cuts and group-selection openings. In our study, chats did nest in one group-selection opening; however, this was the largest (0.76 ha) of the 21 openings. Chats were not observed in any of the other 20 group-openings (all but 1 were <0.4 ha). Prairie Warblers were also observed in two of the group-selection cuts, one of which was the largest opening, while the other was <0.4 ha. Because we monitored nests frequently, we are confident that we spent enough time in the group-selection stands to determine that both Yellow-breasted Chats and Prairie Warblers were indeed absent from the majority of the group-selection openings. In the near future, forest managers in the ONF are considering implementing experimental clear-cuts of intermediate size (2 ha), which may be more suitable for nesting Yellow-breasted Chats and Prairie Warblers. Additional research is needed to evaluate the minimum patch-size requirements for these and other early-successional species.

The change in condition of group-selection stands over time may also be an important factor for early-successional birds. The group-selection stands in this study had been treated only once, and represented a transition phase from an even-aged to an uneven-aged condition. The effects of repeated treatments every 10–15 years are unknown and should be studied. Nevertheless, occupancy and nest-success data are important for early-successional species in transitional group-selection stands because all even-aged stands go through this process when subjected to uneven-aged management.

*Habitat characteristics.*—Although there were a number of significant differences in microhabitat variables at Indigo Bunting nests

in seed-tree versus group-selection openings (Table 2), daily nest survival in the two stand types was similar. Some of these differences are more likely a function of the differences in opening size rather than avian selection for specific nest-site characteristics. The results of regression analyses indicated that most microhabitat variables were similar for successful and failed nests of Indigo Buntings and Yellow-breasted Chats; however, differences in a few key variables may be biologically important to nesting success. Increased vegetative cover surrounding nests explained a large portion of the variation in nest success in group-selection (vine cover) and seed-tree (shrub cover 0.5–1.0 m tall) stands, and for all nests pooled (vine cover). Nests in areas with more vegetative cover may be less conspicuous to some predators. In addition to shrubs, our study areas contained several vine species, especially muscadine grape (*Vitis rotundifolia*), which often afforded excellent vegetative cover.

Logistic regression models also indicated a negative relationship between nest height and probability of nest success for buntings and chats in seed-tree stands. Nests placed lower to the ground may be less conspicuous to some avian predators, which usually detect nests from above. In contrast, Ricketts and Ritchison (2000) found that height of Yellow-breasted Chat nests was greater for successful (median = 0.83 m) than failed (median = 0.75 m) nests in mixed woodland and early-successional habitat in Kentucky. Burhans et al. (2002) also found increased nest predation at Indigo Bunting nests that were lower to the ground. There may be an optimal range of nest height that reduces predation rates in specific habitats, and this may differ among habitat types and geographical locations.

One other habitat variable that may be biologically important to some early-successional species in the ONF is distance to the forest edge. In our study, increased distance to the forest edge was important in explaining nest success for Yellow-breasted Chat in seed-tree stands. Because predation was the primary cause of nest failure for chats, our model suggests that predation may have increased with decreasing distance to the habitat edge. Distance to edge did not explain variation in Indigo Bunting nest success, however. Wood-

ward et al. (2001) also found some evidence of edge effect on Yellow-breasted Chat (but not Indigo Bunting) nest success in the Missouri Ozarks. In that study, chat nests closest to edges ( $\leq 20$  m) had higher predation rates than nests 21–40 m from forest edges. Predation increased, however, at nests  $>40$  m from edges. Other recent studies suggest little or no edge effect associated with openings created by silviculture in predominantly forested landscapes for forest-interior (Hanski et al. 1996, Duguay et al. 2001, Rodewald 2002) and early-successional species (Hanski et al. 1996, King et al. 2001). However, Manolis et al. (2000) showed that many studies that failed to detect edge effects in forested landscapes did not have sufficient power. Other recent studies in forested landscapes have documented mixed results—that is, they showed edge-related increases in nest predation for some species but not others (Burke and Nol 2000, Flaspohler et al. 2001).

*Management implications.*—Our results suggest that group-selection silviculture may not be the most appropriate strategy on the ONF for providing habitat for some early-successional, migratory bird species. If seed-tree cuts are replaced by group-selection cuts on a large scale, this management strategy might reduce availability of nesting habitat for some early-successional species, such as Yellow-breasted Chat and Prairie Warbler. Suitable habitat for these species during the breeding season is important because many have exhibited population declines in Arkansas and elsewhere in recent decades (James et al. 1992, Sauer et al. 2001).

The USFS and other land management agencies have begun to shift their silvicultural practices toward uneven-aged management (Costello et al. 2000). Group-selection silviculture may increase avian abundance and diversity in forested communities because these treatments create habitat for early-successional species while retaining forested habitat and many forest-interior species (Germaine et al. 1997). However, several studies have shown that early-successional species occur less frequently in small forest openings (Annand and Thompson 1997, Rodewald and Smith 1998, Robinson and Robinson 1999). Our data are consistent with these latter findings. Implementation of widespread management tech-

niques in national forests that improve habitat for some species at the expense of other species of conservation concern, such as Yellow-breasted Chat and Prairie Warbler, should be undertaken with the knowledge of the potential negative impacts on those species. Before its widespread adoption, forest managers should understand how group-selection management techniques affect the abundance and diversity of the entire avian community. Implementing a mix of silvicultural techniques may be necessary to maintain populations of early-successional species in the ONF and similar forested landscapes.

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## FLIGHT SPEEDS OF NORTHERN PINTAILS DURING MIGRATION DETERMINED USING SATELLITE TELEMETRY

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**ABSTRACT.**—Speed (km/hr) during flight is one of several factors determining the rate of migration (km/day) and flight range of birds. We attached 26-g, back-mounted satellite-received radio tags (platform transmitting terminals; PTTs) to adult female Northern Pintails (*Anas acuta*) during (1) midwinter 2000–2003 in the northern Central Valley of California, (2) fall and winter 2002–2003 in the Playa Lakes Region and Gulf Coast of Texas, and (3) early fall 2002–2003 in south-central New Mexico. We tracked tagged birds after release and, in several instances, obtained multiple locations during single migratory flights (flight paths). We used data from 17 PTT-tagged hens along 21 migratory flight paths to estimate groundspeeds during spring ( $n = 19$  flights) and fall ( $n = 2$  flights). Pintails migrated at an average groundspeed of  $77 \pm 4$  (SE) km/hr (range for individual flight paths = 40–122 km/hr), which was within the range of estimates reported in the literature for migratory and local flights of waterfowl (42–116 km/hr); further, groundspeed averaged  $53 \pm 6$  km/hr in headwinds and  $82 \pm 4$  km/hr in tailwinds. At a typical, but hypothetical, flight altitude of 1,460 m (850 millibars standard pressure), 17 of the 21 flight paths occurred in tailwinds with an average airspeed of  $55 \pm 4$  km/hr, and 4 occurred in headwinds with an average airspeed of  $71 \pm 4$  km/hr. These adjustments in airspeed and groundspeed in response to wind suggest that pintails migrated at airspeeds that on average maximized range and conserved energy, and fell within the range of expectations based on aerodynamic and energetic theory. Received 19 November 2004, accepted 6 September 2005.

The overall rate at which birds travel during migration, often referred to as migration speed (measured in km/day), includes the time required to accumulate fat reserves and rest prior to migration and at stopovers, and the actual time spent in flight during which fat is catabolized (Alerstam and Lindström 1990). Flight speed (km/hr) is expressed as groundspeed (velocity with respect to ground) or airspeed (velocity with respect to air); the ratio of groundspeed to airspeed directly measures the effects of wind on the energetic costs of migration (Alerstam 1978, Richardson 1990). This ratio is proportional to migration speed (Alerstam 2003), and can predict the strength

of migration (the number of birds aloft; Richardson 1990). For many birds, migration speed may be controlled largely by the time required to acquire fat reserves at stopovers (Alerstam 2003). However, Liechti and Bruderer (1998) concluded that for birds making long nonstop flights, selection of favorable tailwinds to boost groundspeed and save energy (fat) is more important than timing departure based on the rate of fat accumulation. Birds in headwinds, for example, may lower flight altitude until wind velocity declines, thereby increasing groundspeed and conserving energy (Kerlinger and Moore 1989).

Birds migrate at groundspeeds that reflect, among other things, airspeed in the presence or absence of tailwinds or headwinds (Richardson 1990, Alerstam 2003) and aerodynamic characteristics of the species (Pennycuik 1975, Rayner 1990). Aeronautical flight mechanics and bioenergetics theory suggest that birds should fly at one of two characteristic airspeeds during migration. The first minimizes energy cost per unit of time to remain airborne as long as possible (minimum power speed;  $V_{mp}$ ), and the second minimizes the energy cost per unit of distance flown to maximize distance over the ground with a certain fuel load (maximum range speed;  $V_{mr}$ ) (Tucker

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and Schmidt-Koenig 1971, Alerstam and Hedenström 1998). A third conceptual speed, which is not as well defined (Bruderer and Boldt 2001), minimizes total duration of the migration by maximizing overall speed (minimum time speed;  $V_{mt}$ ); however, in practice it is rarely separable from  $V_{mr}$  (Alerstam and Hedenström 1998, Hedenström and Alerstam 1998). In general, waterfowl are well designed for relatively rapid long-distance migration (Rayner 1988), and the moderately sized Northern Pintail (*Anas acuta*), in particular, features an aerodynamic design (streamlined shape, long narrow wings) that supports efficient long-distance flight (Pennycuick 1975, Bellrose 1980, Bruderer and Boldt 2001). However, it is not known whether pintails migrate with flight speeds that adhere to theoretical models.

Investigators have used satellite telemetry to estimate the groundspeeds of migrating swans (*Cygnus* spp.; Pennycuick et al. 1996a, Ely et al. 1997) and Brant (*Branta bernicla*; Green et al. 2002), but we found no such information for ducks. A recent project to track migration of adult female pintails outfitted with satellite-receiving radio tags (platform transmitting terminals; PTTs) in California, Texas, and New Mexico wintering regions (Miller et al. 2001, 2005) provided an opportunity to directly estimate groundspeed. By using archived speeds and directions of winds at a typical waterfowl migration altitude, we then determined their potential airspeed and compared it with theoretical values of  $V_{mp}$  and  $V_{mr}$  (Bruderer and Boldt 2001).

## METHODS

We captured pintails at the following times and locations: (1) December–January 2000–2003 in California at Sacramento Valley national wildlife refuges (NWR) and state wildlife areas (central location: 39° 24' N, 121° 58' W); (2) November–January 2001–2002 in the Playa Lakes Region of Texas at Buffalo Lake NWR (34° 54' N, 102° 7' W) and on private lands (33° 46' N, 101° 51' W), and along the Texas Gulf Coast on a unit of Aransas NWR (28° 33' N, 96° 33' W) and on private lands (27° 20' N, 97° 48' W); and (3) October–November 2001–2002 in New Mexico at Bosque del Apache NWR (33° 48' N, 106°

51' W). These areas are located in important pintail wintering or fall staging regions (Bellrose 1980).

We tagged only adult female pintails because of their critical role in population dynamics (Flint et al. 1998). We sorted all hens by sex and age (Carney 1992), attached federal leg bands, and obtained body mass ( $\pm 5$  g). We used Model 100 PTTs from Microwave Telemetry, Inc. (Columbia, Maryland), and annually attached 25–55 on females in California, 20 in Texas, and 6–9 in New Mexico. The units, with harness and protective neoprene pad, weighed about 26 g, which was 2.7–3.2% of average body mass at capture in California (900–950 g), Texas (820–920 g), and New Mexico (935–975 g), well under commonly used guidelines (Caccamise and Hedin 1985). We attached each PTT dorsally between the wings by fashioning a harness of 0.38-cm-wide (sold as 3/16 in) Teflon ribbon (Bally Ribbon, Bally, Pennsylvania). The completed harness included fore and aft body loops connected with a 1-cm-length of ribbon over the keel, similar to designs used by Malecki et al. (2001). Ours, however, consisted of a single length of ribbon without metal clips, buckles, shrink-tubing, or sewed areas, and we hardened knots with cyanoacrylate glue. We released tagged hens at trap sites 5–19 hr after capture—either during evening pintail flights or at night.

To encompass spring migration, we programmed PTTs to last 6–8 months by using a repeating duty cycle consisting of a 5- to 6-hr transmission period followed by a 72-hr resting period; some PTTs lasted long enough to provide data during fall migration. We used the Argos location and data collection system (Argos, Inc. 1996), including multi-satellite service with standard and auxiliary location processing, to monitor the locations of PTT-tagged pintails. Argos estimates PTT locations from the Doppler shift in transmission frequency received by satellites as they approach and then move away from the PTT. Argos checks the plausibility of locations via (1) minimum residual error, (2) transmission frequency continuity, (3) shortest distance covered since previous location, and (4) plausibility of velocity between locations. The number of positive checks (NOPC; 0–4) is included with each location received via daily

e-mails. The PTTs also provided sensor data to index the unit's temperature, remaining voltage, and motion. We used these, especially the latter, to determine whether birds were alive and to verify that they were flying.

Argos classifies each PTT location based on estimated accuracy and the number of transmissions (messages) received from each PTT during a satellite overpass. The classes of location quality (LC 3, LC 2, LC 1, LC 0) are based on  $\geq 4$  messages received by the satellite via standard data processing; respective accuracies are  $<150$ , 150–350, 350–1,000, and  $>1,000$  m. Accuracy is expressed as the probability that 67% of the locations will fall within stated limits; therefore, high-quality locations might be inaccurate, while lower-quality locations might be very accurate (Hatch et al. 2000). Argos does not estimate accuracy of LC A (3 messages received), LC B (two messages received), or LC Z (latitude/longitude often provided if  $\geq 1$  message received), which are received via auxiliary processing; however, field tests have shown that LC A can be as accurate as LC 0 or LC 1 (Britten et al. 1999, Hays et al. 2001), and LC B can be as accurate or better than LC 0 (Hatch et al. 2000, Hays et al. 2001). Therefore, the accuracy of individual points along a flight path likely varies, even among those of the same LC (Hatch et al. 2000). If a PTT-tagged bird is stationary (not flying), several criteria are normally used to choose one best location from among the many normally provided by Argos (Ely et al. 1997, Butler et al. 1998, Petersen et al. 1999, Hatch et al. 2000). Because of continuous forward travel, however, Argos cannot provide alternate points at each location for pintails in migratory flight. Therefore, we initially plotted all locations of birds in flight and subsequently examined each of them in detail to determine flight paths.

We analyzed and displayed location data using ArcInfo and ArcView Geographic Information System software (Environmental Systems Research Institute, Redlands, California). For each female, we plotted individual flight paths using all PTT locations acquired while the bird was flying. Each flight path consisted of segments formed by successive pairs of adjacent location points (e.g., a path formed by five points would have four flight-path segments). We used only locations re-

corded during pintail migratory flights—identified from multiple locations of birds heading generally northerly or southerly during a single transmission period—concurrently with PTT motion sensor data that suggested vigorous activity. Additionally, we used only locations  $>200$  km from the location recorded on the previous or subsequent (or both) location-days; these criteria precluded inadvertently including stationary pintails or those making only local flights.

We selected only those points that best defined the flight path, and deleted those that deviated from the general line of flight, reversed direction, occurred in clusters (indicating a stationary bird), occurred too close together in space and time, or represented movement too fast or too slow between points—especially if LC was A or worse (Hatch et al. 2000 used LC 0). For example, we considered a given point to be an obvious outlier from the general line of flight if the perpendicular distance from the flight line was greater than the average error distance from true position as determined for the least accurate LCs in recent field tests of PTTs (i.e., 7.5 km for LC 0 and LC A, and 23–35 km for LC B [Blouin et al. 1999, Britten et al. 1999]; 20 km for LC A and LC B [Hatch et al. 2000]; 1–10 km for LC 0 and LC A, and 7 km for LC B [Hays et al. 2001]). We also considered points to be outliers if the time between location points along the path was  $<10$  min and the distances between them  $<20$  km, unless this was typical along the flight path and produced similar intervening groundspeeds among segments. We rejected one of two points that created sharp-angled direction changes (usually  $>45^\circ$ ) and reversals. Additionally, we questioned the accuracy of individual locations if the groundspeed along path segments seemed biologically impossible. We defined this as (1)  $>160$  km/hr, the speed of a Red-breasted Merganser (*Mergus serrator*) flying with a 32 km/hr tailwind, while being chased by a small aircraft (Thompson 1961), or (2)  $<20$  km/hr when point separation was  $<20$  km, unless intervening groundspeeds matched those between other more widely separated points along the path. These criteria are somewhat arbitrary, but provided a consistent method for selecting and rejecting locations—similar to procedures used by Hatch

et al. (2000), in which they discarded locations “conspicuously outside” clusters of points (stationary birds) because they violated their redundancy rule.

We estimated apparent groundspeeds along each outlier-corrected flight path by summing the total time (hr) and distance (km) of each flight-path segment, and then dividing total distance over the flight path by total time from the first to the last accepted location point. We used multiple flight paths from individual tagged hens, if available, and estimated groundspeed as mean  $\pm$  SE for all flights. For comparison, we also estimated groundspeed for all flights using all recorded locations (outliers retained) to recognize our uncertainty with the deletions and determine how our criteria may have affected final groundspeed estimates.

We wanted to determine reliable airspeeds for PTT-tagged pintails, but wind speeds increase and their directions change markedly with increasing altitude (Kerlinger and Moore 1989, Ahrens 2000); in addition, we did not know at what altitudes our tagged ducks migrated (our PTTs did not have altitude sensors). We had no means to predict when or where measurable flight paths would occur, and as a result, we could not *a priori* deploy radar and weather balloons to obtain groundspeed, wind speed, wind direction, and flight altitude simultaneously, as done when birds pass predictable locations (Bruderer and Boldt 2001). Therefore, to assess the effect of headwinds or tailwinds along the 21 pintail flight paths, we assumed migration altitudes of sea level and 1,460 m above sea level (1,000 and 850 millibars [mb] at standard pressure; Ahrens 2000), which is within the typical range used by migrating waterfowl (Kerlinger and Moore 1989, Berthold 1996), and for which archived weather data were readily available. The higher altitude was used by Dau (1992), Shamoun-Baranes et al. (2003), and Gill et al. (2005) to examine migration of Brant, White Storks (*Ciconia ciconia*), and Bar-tailed Godwits (*Limosa lapponica*), respectively. We obtained wind speed and direction on the dates of pintail flights using North American Constant Pressure weather charts (850 mb) for 00:00 UTC and 12:00 UTC, published by the National Center for Environmental Prediction (NCEP; National Climatic Data Center 2005).

We assumed that the weather charts represented conditions at the location of flying pintails, and we used wind speeds and directions nearest to each pintail flight path (Shamoun-Baranes et al. 2003). Because exact flight altitudes remained unknown, we did not add unjustified precision to the generally imperfect data to account for the angle at which tailwinds or headwinds may have intercepted pintail flight paths (Gill et al. 2005). Instead, we assumed that tailwinds and headwinds essentially paralleled flight paths, and ignored compensation and drift (Wege and Raveling 1984, Alerstam and Hedenström 1998). We calculated airspeeds either as (1) groundspeed  $-$  tailwind or (2) groundspeed  $+$  headwind. To characterize migration conditions at the surface, we obtained archived sky conditions and surface wind speed and direction at the time of flights from weather stations nearest the flight paths (Weather Underground 2005).

## RESULTS

During 2001, 2002, and 2003, we obtained 21 flight paths of 17 PTT-tagged pintails for which we estimated groundspeeds (Fig. 1). Of this total, 19 flights from 16 pintails occurred during spring, and 2 flights from 2 birds occurred during fall (1 hen provided 1 spring and 1 fall flight; Table 1). These data included 14 pintails tagged in California, 2 in Texas, and 1 in New Mexico. We used all original Argos locations from 10 pintail flight paths (uncorrected), but deleted  $\geq 1$  location from each of 11 others (outlier-corrected), because they did not meet our established criteria. Outlier correction resulted in increases in groundspeed of 4–21 km/hr for five flight paths, decreases in speed of 1–69 km/hr for five flight paths, and no change for one flight path. Outlier correction reduced our total number of locations from 108 to 77. Correction for outliers did not markedly increase the proportion of high-quality locations forming flight paths compared with that in the uncorrected data set. For example, the proportion of LC 1 and LC 2 locations increased to 17% from 12% of all locations, and those of LC A, B, and Z declined to 25% from 32% (no change in proportion of LC 0).

When we used the 11 outlier-corrected flights and the 10 uncorrected flights, groundspeeds of pintails along all 21 flight paths



FIG. 1. Migration flight paths and path segments of adult female Northern Pintails PTT-tagged in California, Texas, and New Mexico, used to estimate groundspeed and airspeed (km/hr), 2001–2003. Circled uppercase letters are bird identifiers from Tables 1, 2. Thick black lines show the measured flight paths divided into segments by open circles representing pintail locations. Thin gray lines show migration routes prior and subsequent to the measured path.

ranged from 40 to 122 km/hr (Table 1) and averaged  $77 \pm 4$  km/hr (CV = 5.6, 90% CI = 69–84). Two-thirds of the speeds (14 of 21 flight paths) occurred over a narrower range of 61–80 km/hr. Without omitting outliers,

groundspeeds ranged from 45 to 111 km/hr and averaged  $78 \pm 4$  km/hr (CV = 4.9, CI = 72–84), indistinguishable from the outlier-corrected value. Groundspeed averaged  $75 \pm 4$  km/hr (CV = 4.6, CI = 70–81) for the 10

TABLE 1. Outlier-corrected groundspeeds of adult female Northern Pintails, including start and end times, distance flown, and time in flight, along flight paths determined via satellite telemetry, 2001–2003. All times are Pacific Standard Time, except as noted. Bird identifiers (uppercase letters) correspond to those in Figure 1.

Year	Start date	Bird	Location of flight ( $n_1, n_2$ ) <sup>a</sup>	Start-end times	Distance flown (km)	Time in flight (hr)	Ground speed (km/hr)
2001	21 Mar	A	West-central Idaho (4, 4)	04:15–08:42 <sup>e</sup>	288.7	4.45	65
2001	25 Apr	B	West of Washington/British Columbia (8, 6)	03:55–09:23	393.3	5.45	72
2001	27 Apr	C	Northeastern Alberta (10, 5)	04:29–07:58 <sup>e</sup>	267.4	3.49	77
2001	27 Apr	D	Western Alberta (4, 4)	19:31–00:38 <sup>e</sup>	511.4	5.12	100
2001	3 May	E	West of Washington/Oregon (4, 4)	02:30–06:23	309.2	3.90	79
2002	23 Feb	F	Northern California (8, 3)	17:05–20:06	212.6	3.13	68
2002	20 Mar	G	Southern Idaho (4, 3)	01:09–03:42 <sup>e</sup>	294.4	2.55	116
2002	21 Mar	H <sup>b</sup>	Eastern Oregon to western Idaho (3, 3)	19:55–23:57 <sup>e</sup>	257.8	4.03	64
2002	13 Apr	I	North Dakota (10, 5)	15:54–19:52 <sup>f</sup>	180.1	2.28	79
2002	19 Apr	J	British Columbia coast (7, 4)	02:20–07:13	216.3	4.89	44
2002	21 Apr	K <sup>c</sup>	West of Washington/British Columbia (8, 5)	11:51–15:46	157.6	3.91	40
2002	24 Apr	L <sup>d</sup>	Western Oregon/ocean (3, 3)	23:17–01:25	292.7	3.79	77
2002	25 Apr	M	Eastern Texas (3, 3)	20:41–22:20 <sup>f</sup>	218.3	3.06	71
2002	8 May	N <sup>b</sup>	Central Alberta (3, 3)	21:08–22:49 <sup>e</sup>	206.1	3.36	62
2002	9 May	O	Central Oregon (2, 2)	21:35–23:14	127.4	1.66	77
2002	14 May	P <sup>b</sup>	Southeastern Yukon (9, 5)	09:08–10:48	366.4	3.01	122
2002	26 May	Q <sup>c</sup>	West-central British Columbia (4, 3)	22:47–02:15	277.3	3.46	80
2002	10 Oct	R <sup>d</sup>	Western Oregon/ocean (3, 2)	21:38–23:16	99.8	1.64	61
2002	12 Nov	S	Southern New Mexico to Mexico (6, 5)	18:49–22:17 <sup>e</sup>	428.1	4.51	95
2003	19 Mar	T	Northeastern Oregon (2, 2)	01:07–02:46	135.3	1.66	82
2003	31 Mar	U	Eastern Oregon (3, 3)	19:28–22:39	243.1	3.19	76

<sup>a</sup>  $n_1$  = total number of separate location points recorded during flight and used to estimate groundspeed without correcting for outliers;  $n_2$  = number of accepted location points used to estimate outlier-corrected groundspeed.

<sup>b,c,d</sup> Superscripts of the same letter indicate multiple flights for the same pintail.

<sup>e</sup> Mountain Standard Time.

<sup>f</sup> Central Standard Time.

uncorrected flights,  $78 \pm 8$  km/hr (CV = 10.1, CI = 65–90) for the 11 outlier-corrected flights, and  $80 \pm 7$  km/hr (CV = 8.4, CI = 69–91) for the 11 flights when not corrected for outliers. Most (19 of 21) flights occurred partially or entirely at night (Table 1), and two paths transited land and sea (Fig. 1).

Based on wind speeds and directions at 1,400 m (850 mb), 17 of the 21 flights (81%) occurred in tailwinds and four in headwinds (Table 2). Groundspeeds averaged  $82 \pm 4$  km/hr (CV = 8.2, CI = 75–89) in tailwinds and  $53 \pm 6$  km/hr (CV = 11.8, CI = 43–63) in headwinds. Three of the four flights that occurred in headwinds at 850 mb (birds A, J, and K; Table 2) would have had tailwinds near the ground surface of 6–13, 7–11, and 13–15 km/hr, respectively (weather station

data), and the fourth flight (bird N) would have had headwinds of 6–9 km/hr. Corresponding airspeeds of pintails at 850 mb ranged from 24 to 97 km/hr in tailwinds and from 59 to 80 km/hr in headwinds (Table 2), with means of  $55 \pm 4$  km/hr (CV = 7.9, CI = 48–62) in tailwinds and  $71 \pm 4$  km/hr (CV = 6.2, CI = 64–78) in headwinds. The ratios of groundspeed to airspeed averaged  $0.73 \pm 0.6$  in headwind (CV = 8.2, CI = 0.63–0.83) and  $1.61 \pm 0.14$  in tailwind (CV = 8.5, CI = 1.39–1.83).

The longest distance flown by a pintail for which we estimated groundspeed (bird B), was 2,926 km—from Goose Lake in southern Oregon ( $42^\circ 15' N$ ,  $120^\circ 23' W$ ) to the Kenai Peninsula in Alaska ( $59^\circ 12' N$ ,  $151^\circ 46' W$ ; Table 1). Assuming that pintails flew at the

TABLE 2. Airspeeds of adult female Northern Pintails estimated using satellite telemetry and supporting wind speed and direction data from North American Constant Pressure weather charts (850 millibars or 1,460 m), 2001–2003. Local sky and surface wind direction categories at weather stations nearest to flight paths are also given. Bird identifiers (uppercase letters) correspond to those in Figure 1.

Year	Date	Bird	Ground-speed (km/hr) <sup>a</sup>	Highest wind speed (km/hr) <sup>b</sup>	Wind direction (compass) <sup>b</sup>	Wind category <sup>c</sup>	Airspeed (km/hr) <sup>d</sup>	Local sky conditions; surface wind category <sup>e</sup>
2001	21 Mar	A	65	9	NW	QHW	74	MC; QTW <sup>1</sup>
2001	25 Apr	B	72	37	SSW	QTW	35	OC; QHW <sup>2</sup>
2001	27 Apr	C	77	19	SSW	QTW	58	OC; QTW <sup>3</sup>
2001	27 Apr	D	100	28	SSW	QTW	72	MC; none <sup>4</sup>
2001	3 May	E	79	46	SSW	QTW	33	PC; QTW <sup>2</sup>
2002	23 Feb	F	68	19	SSE	TW	49	OC; VAR <sup>5</sup>
2002	20 Mar	G	116	19	W	TW	97	CL; QTW <sup>6</sup>
2002	21 Mar	H <sup>f</sup>	64	28	SW	QTW	36	CL; QHW <sup>7</sup>
2002	13 Apr	I	79	28	SW	QTW	51	PC; TW <sup>8</sup>
2002	19 Apr	J	44	28	WNW	QHW	72	MC; QTW <sup>9</sup>
2002	21 Apr	K <sup>g</sup>	40	19	NNW, N	HW	59	LR; QTW <sup>10</sup>
2002	24 Apr	L <sup>h</sup>	77	19	SW	QTW	58	CL; VAR <sup>11</sup>
2002	25 Apr	M	71	28	WSW, SW	QTW	43	MC; QHW <sup>12</sup>
2002	8 May	N <sup>f</sup>	61	19	N	HW	80	OC; HW <sup>4</sup>
2002	9 May	O	77	9	SE	TW	68	OC; HW <sup>13</sup>
2002	14 May	P <sup>f</sup>	122	56	SE	TW	66	LR; QTW <sup>14</sup>
2002	26 May	Q <sup>g</sup>	80	56	SSE	TW	24	LR; QTW <sup>15</sup>
2002	10 Oct	R <sup>h</sup>	61	9	NW, NNW	TW	52	OC; none <sup>11</sup>
2002	12 Nov	S	95	28	NNW, N	QTW	67	CL; QTW <sup>16</sup>
2003	19 Mar	T	82	19	SSW	TW	63	CL; QTW <sup>17</sup>
2003	31 Mar	U	76	9	SW	QTW	67	R; QTW <sup>18</sup>

<sup>a</sup> Values rounded to nearest km/hr from Table 1.

<sup>b</sup> Wind speeds and compass directions obtained from airspeed/direction symbols on 850 mb constant pressure weather charts nearest pintail flights.

<sup>c</sup> Symbols for relative wind direction category apply to upper air and surface data: Q = quartering, TW = tailwind, HW = headwind, SW = sidewind, VAR = variable, none = calm.

<sup>d</sup> Airspeed = groundspeed – tailwind, or groundspeed + headwind; wind speed used is the highest of the ranges obtained from weather charts.

<sup>e</sup> Sky conditions: OC = overcast, LR = light rain, R = rain, MC = mostly cloudy, PC = partly cloudy, CL = clear, where >1 condition applied, we show the condition least favorable for migration. Numbered superscripts refer to the nearest weather station: 1 = Boise, Idaho; 2 = Hoquiam, Washington; 3 = Fort Smith, Northwest Territories; 4 = Edmonton, Alberta; 5 = Redding, California; 6 = Burley, Idaho; 7 = Ontario, Oregon; 8 = Jamestown, North Dakota; 9 = Vancouver, British Columbia; 10 = Quillayute, Washington; 11 = Newport, Oregon; 12 = College Station, Texas; 13 = Redmond, Oregon; 14 = Watson Lake, Yukon; 15 = Terrace, British Columbia; 16 = Truth or Consequences, New Mexico; 17 = Hermiston, Oregon; 18 = Burns, Oregon.

<sup>f,g,h</sup> Superscripts of the same letter indicate multiple flights for the same pintail.

average outlier-corrected groundspeed of 77 km/hr, they would have required 38 hr to complete the flight nonstop.

## DISCUSSION

The estimated 77 km/hr migration groundspeed of PTT-tagged adult female pintails was consistent with that of the upper range of pintail groundspeeds (local flights) estimated using radar (65–76 km/hr; Bruderer and Boldt 2001). Average groundspeeds of other ducks during local flights have ranged from 42 to 116 km/hr (Speirs 1945, Lokemoen 1967, Kerlinger 1995, Bruderer and Boldt 2001), very similar to the range we obtained for migrating pintails. During migration, PTT-tagged Whooper (*Cygnus cygnus*) and Tundra (*C. columbianus*) swans migrated at 60–90 km/hr (Pennycuick et al. 1996a, Ely et al. 1997), and

Canada Geese (*Branta canadensis*) fitted with VHF radio-transmitters migrated at groundspeeds of 49–110 km/hr (Wege and Raveling 1984). Bellrose and Crompton (1981) clocked migrating Canada Geese at 61–73 km/hr, Lesser Snow Geese (*Chen caerulescens*) at 67–83 km/hr, and Mallards (*Anas platyrhynchos*) at 72 km/hr by following in automobiles or aircraft. Using satellite telemetry, radar, and other means, migrating Brant have been recorded at groundspeeds of 99 km/hr (Dau 1992), 90 km/hr (Lindell 1977 cited in Ebbing and Spaans 1995), 30–115 km/hr (Green and Alerstam 2000), and 58–109 km/hr (Green et al. 2002). Wide interspecific variation in these reported groundspeed estimates probably resulted from species-specific flight aerodynamics (Pennycuick 1975, Rayner 1990), atmospheric conditions (Kerlinger and

Moore 1989), and errors associated with the various methods (Bruderer and Boldt 2001). The relatively wide range of pintail groundspeeds in our study undoubtedly reflected primarily wind conditions, and perhaps angle of flight (ascending, descending, horizontal; Green and Alerstam 2000); however, the close agreement between outlier-corrected and uncorrected data suggests that measurement error was minimal. We recommend that investigators report groundspeeds and groundspeed to airspeed ratios because of their implication in analysis of flight range and cost.

Birds use tailwinds to minimize the energetic cost of migration by increasing groundspeed and range, reducing airspeed to maintain groundspeed, or both (Richardson 1990, Alerstam and Hedenström 1998), and this has been verified for migrating waterfowl (Blokpoel 1974, Bellrose and Crompton 1981, Wege and Raveling 1984, Dau 1992, Green et al. 2002). Most pintails (had they migrated at our specified altitude of 1,460 m) would have benefited from tailwinds, as exemplified by their average higher groundspeed and lower airspeed in tailwinds. Birds are known to alter flight altitudes and move to those with favorable winds (Gauthreaux 1991). If three of the four pintails in our study that we assumed were flying into headwinds aloft had instead been flying near the ground surface, they would have had tailwinds. Also, the three flights occurred partially or completely during the day (Table 1), when low-altitude migration flights are typical (Richardson 1990). However, we cannot be sure of the migration altitude, and sky conditions observed from the ground varied from mostly cloudy to light rain and overcast (Table 2), weather types that tend to discourage migration (Richardson 1990).

Birds generally adjust airspeed when wind direction changes; waterfowl increase airspeed to compensate for headwinds and reduce airspeed as tailwinds increase (Tucker and Schmidt-Koenig 1971, Bellrose and Crompton 1981, Wege and Raveling 1984, Pennycuick et al. 1996a), but the adjustments are not necessarily proportionate (Bellrose and Crompton 1981). Our pintails clearly did not have a strategy to maintain airspeeds in changing wind conditions (Table 2), although Blokpoel (1974) concluded that migrating Lesser Snow Geese did. Our estimates of av-

erage pintail airspeed support the hypothesis that their airspeed was faster, and groundspeed slower, in headwinds compared with tailwinds. The ratios of groundspeed to airspeed for tagged pintails show that compared with still air (ratio = 1.0), pintails decreased their groundspeeds about 27% in headwinds and increased groundspeeds by about 61% in tailwinds, suggesting that migration occurred at  $V_{mr}$ . Demonstrating such compensation during local flights, Tucker and Schmidt-Koenig (1971) reported a pintail airspeed of  $56 \pm 1$  km/hr with tailwinds and  $66 \pm 1$  km/hr against headwinds, similar to our results (55 and 71 km/hr, respectively). Because Tucker and Schmidt-Koenig (1971) did not report respective groundspeeds or wind directions, we estimated groundspeeds from their study by using their reported average wind speeds of 18 and 31 km/hr and applying them as tailwinds and headwinds. This produced potential respective groundspeeds of 74 and 87 km/hr in tailwinds and 48 and 35 km/hr in headwinds, similar to our findings.

Using the theoretical flight models of Pennycuick (1989) and Rayner (1990), Bruderer and Boldt (2001) calculated  $V_{mr}$  and  $V_{mp}$  for pintails as 64 and 40 km/hr, respectively. The average airspeed of our pintails in tailwinds (55 km/hr) was above  $V_{mp}$  and below  $V_{mr}$ , and their average airspeed in headwinds (71 km/hr) was greater than both  $V_{mp}$  and  $V_{mr}$ . In four instances, our pintails flew more slowly than  $V_{mp}$  in tailwinds (24–36 km/hr), and on nine flight paths in variable wind directions, they flew faster than  $V_{mr}$  (66–97 km/hr); on eight paths, pintails flew at speeds between the theoretical speeds (43–63 km/hr; Table 2). Our data support Welham's (1994) findings that pintail-sized birds tend to migrate at  $V_{mr}$ , but are not bound by theoretical flight models (Pennycuick 1998); more data are needed to compare field results with their predictions. The four excessively slow speeds in tailwinds ( $<V_{mp}$ ) may reflect errors resulting from overestimation of wind speed (Tucker and Schmidt-Koenig 1971), resulting from potential differences between winds at the actual (unknown) and selected (850 mb) flight altitudes. Pintails probably do not fly at the theoretical minimum power speed in any event, a phenomenon demonstrated for a Common Teal (*Anas crecca crecca*) and other birds that

refused to fly in wind tunnels at  $V_{mp}$  (Penny-cuick et al. 1996b). To address this problem in future field studies, wind speeds and directions will need to be obtained very near flight altitudes because wind data gleaned from constant pressure charts are only as relevant as the selected flight altitude. Investigators could use PTTs with onboard altitude sensors, but these sensors are not yet available for the small PTTs required for use on pintail-sized birds. Larger PTTs with GPS technology are available, which would be suitable for geese and swans; these can track position, altitude, heading, and speed with high accuracy ( $\pm 30$  m; Microwave Telemetry, Inc. 2005).

Most waterfowl are known to migrate at night as well as during daylight hours (Bellrose 1980, Kerlinger and Moore 1989). Therefore, it is not surprising that nearly all of our measured flights of tagged pintails occurred partially or entirely at night. For long-distance migrations, typically beginning after sunset (Kerlinger and Moore 1989), travel may extend into daylight hours because there is not enough time to make the transit during nighttime hours (Berthold 1996), or wind conditions might favor continuing into daytime hours (Liechti and Schaller 1999 cited in Jenni and Schaub 2003); five of our recorded flights overlapped day and night (birds A, B, C, E, and J; Table 1). Migration in the cooler, ambient nighttime air at moderate to high altitudes theoretically provides bioenergetic benefits of heat dissipation and water conservation through evaporative cooling (Berthold 1996, Kvist et al. 1998). This could be critical for waterfowl during long, nonstop migrations when diurnal and surface temperatures are high (e.g., early fall, late spring). Nocturnal atmospheric conditions provide distinct advantages to migrating birds, including cooler temperatures and more humidity, denser air, weaker and more laminar horizontal winds, and little or no vertical air motion compared with daytime conditions (Kerlinger and Moore 1989, Ahrens 2000); these conditions maximize flight speed while reducing energy cost. Additionally, night migration would enable celestial navigation (Bellrose 1980).

Our data suggest that researchers need not delete any but the most obvious outliers to estimate groundspeeds when using the method of total distance divided by total time with

relatively large sample sizes. Average ground-speed estimated using all data did not differ from that using outlier-corrected data, even though the former included very high and unrealistic speeds on six flight-path segments (175, 381, 484, 611, 829, and 999 km/hr). These did not affect the average because they occurred over very short time periods between the first and last location points (32 sec to 7.2 min), and because we did not estimate groundspeed by averaging speeds of each flight-path segment. Investigators could increase the frequency of high-quality locations ( $LC > 0$ ) by increasing PTT power, or, for large species, adopt new PTT models that incorporate global positioning systems (GPS; Microwave Telemetry, Inc. 2005). This would improve estimation of groundspeeds and airspeeds and their precision along individual flight-path segments.

Back-mounted PTTs may have reduced our estimates of pintail groundspeed; however, results from previous studies that addressed this issue have been inconclusive. For example, Butler et al. (1998) estimated a potential 5% increase in the energetic costs of flight of Barnacle Geese (*Branta leucopsis*) outfitted with 33-g PTTs. Because geese are able to reposition PTTs under their body feathers while preening (Butler et al. 1998), wind resistance due to PTTs may be reduced (Obrecht et al. 1988). Harnessed transmitters increased the energy cost of rapid flight in homing pigeons (Rock Pigeon, *Columba livia*; Gessaman and Nagy 1988), perhaps due to the vertically flattened posterior ends of the test transmitters (Obrecht et al. 1988). In wind tunnel experiments that tested the aerodynamic characteristics of three transmitter sizes attached to frozen Lesser Snow Geese and Mallards, streamlined transmitters created the least drag, and the smallest test transmitters (slightly larger than our 20-g unit [excluding harness]) created drag too small to be measured (Obrecht et al. 1988); the sloped anterior and posterior ends of our pintail PTTs mimicked the streamlined shape of these units. Penny-cuick et al. (1996b) recently reduced their estimate of body-drag coefficients for flying birds from 0.4 to 0.08, suggesting that drag may not be as important as once thought. Based on this new information and our typical mean groundspeeds and airspeeds of PTT-tagged

pintails, we conclude that the variation in groundspeed caused by wind direction and speed likely overwhelmed wind resistance and mass effects of PTTs. Nonetheless, we encourage researchers to develop reliable, implantable PTTs for moderately sized waterfowl because of potential aerodynamic benefits and reduced energetic costs of flight.

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## HOST USE BY SYMPATRIC COWBIRDS IN SOUTHEASTERN ARIZONA

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**ABSTRACT.**—Sympatric avian brood parasites may compete for the same nests to parasitize. Host-resource partitioning, or “alloxenia,” is exhibited by several Old World cuckoos where they are sympatric in Africa, Japan, and Australia. I examined host use by sympatric Brown-headed Cowbirds (*Molothrus ater*) and Bronzed Cowbirds (*M. aeneus*) from 1997 to 1999 in pine-oak and montane riparian forests in southeastern Arizona. Bronzed and Brown-headed cowbirds partitioned hosts by host body size. Brown-headed Cowbirds did not parasitize larger hosts (i.e., Western Tanager, *Piranga ludoviciana*; and Hepatic Tanager, *P. flava*), while Bronzed Cowbirds did not parasitize smaller hosts (i.e., Painted Redstarts, *Myioborus pictus*; and Bell’s Vireos, *Vireo bellii*). Although there was some host overlap (only 2/7 parasitized host species were parasitized by both cowbird species), only 3/48 nests (all Plumbeous Vireo, *V. plumbeus*) contained eggs of both parasite species. Parasitism by sympatric cowbirds in southeastern Arizona appears to fit the pattern of alloxenia. Received 16 October 2003, accepted 13 June 2005.

Avian obligate brood parasites do not build nests, but lay their eggs in the nests of other species, the “hosts,” which raise young parasites (Friedmann 1929, Davies 2000). Fitness of obligate brood parasites is directly related to choosing suitable hosts. Such hosts lack effective anti-parasite behaviors (e.g., egg rejection; Rothstein 1990), effectively incubate the parasite’s eggs, and feed the parasite’s young an appropriate diet (Middleton 1991). Interference by other brood parasites at an already parasitized host nest—in the form of egg puncturing, egg removal, or multiple parasitisms—can reduce parasite fitness (Peer and Sealy 1999, Nakamura and Cruz 2000, Trine 2000).

Partitioning of hosts may reduce the potential costs of interference competition between sympatric brood parasites. Sympatric brood parasitic cuckoos (*Cuculus*, *Chrysococcyx*, *Clamator*, *Eudynamis*, *Oxylophus*, *Scythrops*) in Africa, Australia, and Japan partition their primary hosts, possibly reducing competition for nests (Friedmann 1967, Payne and Payne 1967, Brooker and Brooker 1989, 1992; Higuchi 1998). Friedmann (1967) coined the terms “alloxenia” to describe host partitioning by obligate brood parasites in sympatry and “homoxenia” to describe overlap in host

use. In contrast to studies of Old World cuckoos, there is little information on host use by sympatric New World brood parasites (but see Carter 1986, Peer and Sealy 1999, Mermoz and Fernández 2003).

The brood-parasitic Brown-headed (*Molothrus ater*) and Bronzed (*M. aeneus*) cowbirds are sympatric in the southern United States and northern Mexico (Lowther 1993, 1995). Bronzed and Brown-headed cowbirds are considered host generalists that have been recorded parasitizing 94 and 230 different host species, respectively; they overlap in the parasitism of 37 species (Sealy et al. 1997, Ortega 1998; P. E. Lowther pers. comm.). The reproductive success of female cowbirds is directly related to the number of eggs laid in appropriate host nests during the host’s laying period (Ortega 1998). Body size of the host also may affect the reproductive success of parasites: relatively small hosts may not be able to effectively incubate the larger eggs of parasites (Davies and Brooke 1988, McMaster and Sealy 1997, Peer and Bollinger 1997), whereas large hosts may be able to grasp and eject cowbird eggs (Rothstein 1975, Rohwer and Spaw 1988). Host selection may differ between the two cowbird species because Bronzed Cowbirds are larger (female mass = 56.9 g) than Brown-headed Cowbirds (female mass = 32.0 g; Johnsgard 1997).

Similar to sympatric species of brood parasites elsewhere (e.g., Brooker and Brooker 1992), coexisting cowbirds may reduce potential interspecific competition for nests through

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differential host use (i.e., allolexenia). I tested the hypothesis that sympatric Bronzed and Brown-headed cowbirds exhibit host-size allolexenia in southeastern Arizona.

## METHODS

*Study sites.*—My study was conducted in the Huachuca Mountains (elevation 1,500–2,450 m, 31° 26' N, 110° 20' W) of southeastern Arizona near Sierra Vista. During the breeding seasons (May–July) of 1997–1999, I examined host use by Bronzed and Brown-headed cowbirds at four discrete study sites (~20 ha each) in two distinct habitat types: Reef Townsite and Sawmill Canyon in pine-oak woodlands, and Garden Canyon and Huachuca Canyon in montane riparian forests. The two montane riparian forest sites were 7 km apart, and the pine-oak woodland sites were 9 km apart. Of the four sites, Garden Canyon and Sawmill Canyon were closest to one another (1.5 km apart).

The overstory in the pine-oak woodland sites was dominated by ponderosa (*Pinus ponderosa*), southwestern white (*P. strobiformis*), Apache (*P. latifolia*), and Chihuahuan (*P. chihuahuana*) pines. Dominant shrubs of the understory included silverleaf (*Quercus hypoleucoides*) and netleaf (*Q. reticulata*) oaks, and, especially at Reef Townsite, manzanita (*Arctostaphylos pungens*).

Montane riparian habitat is narrow, linear (<200 m wide), and extends along an elevational gradient (1,500–1,800 m) surrounded by a matrix of xeric habitats: pinyon-juniper, desert scrub, montane chaparral, desert grassland, and Madrean oak woodlands. Primary canopy species included Fremont cottonwood (*Populus fremontii*), velvet ash (*Fraxinus velutina*), Arizona sycamore (*Platanus wrightii*), bigtooth maple (*Acer grandidentatum*), and Arizona walnut (*Juglans major*). Common in the understory were Arizona white (*Q. arizonica*) and netleaf oaks, Arizona madrone (*Arbutus arizonica*), silk-tassel (*Garrya wrightii*), poison ivy (*Rhus radicans*), and canyon grape (*Vitis arizonica*).

*Frequency of host parasitism, impact, and cowbird reproductive success.*—Searches for potential host nests were conducted daily from 20 May to 15 July at Reef Townsite and Sawmill Canyon during 1997–1999, and in Huachuca Canyon and Garden Canyon during

1998–1999. Potential nests included those of all known host species (Ortega 1998) and congeners of known hosts. Nests were monitored at least once every 3 days, either directly or with a 6-m telescoping mirror-pole. I defined the frequency of parasitism as the proportion of parasitized nests. Clutch initiation was determined by backdating from the hatching date, using published incubation information (Ehrlich et al. 1988). The frequency of cowbird and host egg laying was standardized into 10-day periods across the total pool of nests. Cowbird egg-laying patterns then were compared with host clutch initiation by size classes of hosts (small: <10 g; medium: 10.0–29.9 g; large: >30 g).

*Statistical analysis.*—To determine whether Bronzed and Brown-headed cowbirds laid their eggs randomly (i.e., the “shotgun” approach; Kattan 1997) among host nests, I compared cowbird laying patterns to both a typical Poisson distribution (Preston 1948, Mayfield 1965, Elliott 1977, Kattan 1997, Trine 2000) and an adjusted Poisson distribution (Lowther 1984, Lea and Kattan 1998). Unparasitized nests are a special case because some of them may be found by cowbirds and not selected, or found too late in the egg-laying cycle to parasitize (Lowther 1984, Lea and Kattan 1998). Following Lea and Kattan (1998), I calculated the proportion of nests without cowbird eggs based on the distribution of nests with cowbird eggs. A Poisson distribution adjusted for zero-class parasitism can serve as a more conservative measure of cowbird egg-laying patterns, where a significant departure of the observed distribution from the Poisson suggests that cowbirds target nests. I used the Kolmogorov-Smirnov test (Zar 1984) to compare the distribution of Bronzed and Brown-headed cowbird egg laying, nonparametric rank sum tests to compare central tendencies when data were not normally distributed, and likelihood tests (*G*-tests) adjusted with William’s correction (Sokal and Rohlf 1981). Unless otherwise stated, all values are reported as mean  $\pm$  SD; statistical significance was set at  $P = 0.05$ . For statistical analysis, I used the software package JMP (SAS Institute, Inc. 1995).

## RESULTS

*Parasitism frequency.*—I monitored 220 nests of 15 species (Table 1); 8 species were

TABLE 1. Frequency of Bronzed and Brown-headed cowbird parasitism, Huachuca Mountains, Arizona, 1997–1999.

Host species	Mass (g) <sup>a</sup>	Total nests <i>n</i> (%)	Nests parasitized	
			Bronzed Cowbird <i>n</i> (%)	Brown-headed Cowbird <i>n</i> (%)
Hosts parasitized by both cowbird species				
Hutton's Vireo	11.6	6 (2.7)	3 (50.0)	2 (33.3)
Plumbeous Vireo	16.6	68 (30.9)	7 (10.3)	22 (32.3)
Subtotal		74 (33.6)	10 (13.5)	24 (32.4)
Hosts parasitized by Bronzed Cowbirds only				
Warbling Vireo	14.8	1 (0.4)	1 (100)	
Western Tanager	28.1	5 (2.3)	1 (20.0)	
Hepatic Tanager	38.0	8 (3.6)	6 (75.0)	
Subtotal		14 (6.4)	8 (57.1)	
Hosts parasitized by Brown-headed Cowbirds only				
Painted Redstart	7.9	7 (3.2)		1 (14.3)
Bell's Vireo	8.5	12 (5.4)		8 (75.0)
Subtotal		19 (8.6)		9 (47.4)
Species not parasitized				
Buff-breasted Flycatcher	7.9	16 (7.3)		
Western Wood-Pewee	12.8	37 (16.8)		
Yellow-eyed Junco	20.4	8 (3.6)		
Greater Pewee	27.2	28 (12.7)		
Black-headed Grosbeak	42.2	18 (8.2)		
Cassin's Kingbird	45.6	3 (1.4)		
Mexican Jay	124.0	1 (0.4)		
Steller's Jay	128.0	2 (0.9)		
Subtotal		113 (51.4)		
Total <sup>b</sup>		220 (100)	18 (8.2)	33 (15.0)

<sup>a</sup> Bird mass data from Dunning (1993).

<sup>b</sup> Although cowbirds parasitized 48 nests, the overlapping parasitism at three Plumbeous Vireo nests raises the total to 51 instances of nest parasitism among the 48 nests.

not parasitized ( $n = 113$  nests) and 7 species were parasitized ( $n = 107$  nests of host species;  $n = 45$  at Reef Townsite, 21 at Sawmill Canyon, 22 at Huachuca Canyon, and 19 at Garden Canyon). Forty-five percent (48/107) of all host nests were parasitized; two host species were parasitized by both cowbird species (Hutton's Vireo, *Vireo huttoni*; and Plumbeous Vireo, *Vireo plumbeus*), and three nests (all Plumbeous Vireo) contained at least one egg of both cowbird species (Table 1). For hosts parasitized by both species, Bronzed Cowbird parasitism (13.5%, 10/74) was less than half that of Brown-headed Cowbirds (32.4%, 24/74; Table 1). Only Bronzed Cowbirds parasitized Hepatic Tanager (*Piranga flava*; large host) and Western Tanager (*P. ludoviciana*; high end of medium-size class), and only Brown-headed Cowbirds parasitized

Painted Redstart (*Myioborus pictus*) and Bell's Vireo (*Vireo bellii*; Table 1). Two of the medium-sized hosts (Hutton's Vireo, *Vireo huttoni*, and Plumbeous Vireo) were parasitized by both cowbird species, and the Warbling Vireo (*Vireo gilvus*) was parasitized only by the Bronzed Cowbird (Table 1).

Potential host nests monitored, but not parasitized, included those of Buff-breasted Flycatcher (*Empidonax flavifrons*), Western Wood-Pewee (*Contopus sordidulus*), Greater Pewee (*C. pertinax*), Cassin's Kingbird (*Tyrannus vociferans*), Mexican Jay (*Aphelocoma ultramarina*), Steller's Jay (*Cyanocitta stelleri*), Yellow-eyed Junco (*Junco phaeonotus*), and Black-headed Grosbeak (*Pheucticus melanocephalus*; Table 1). Other known cowbird hosts (Ortega 1998) commonly observed on at least two of the study sites, but for which

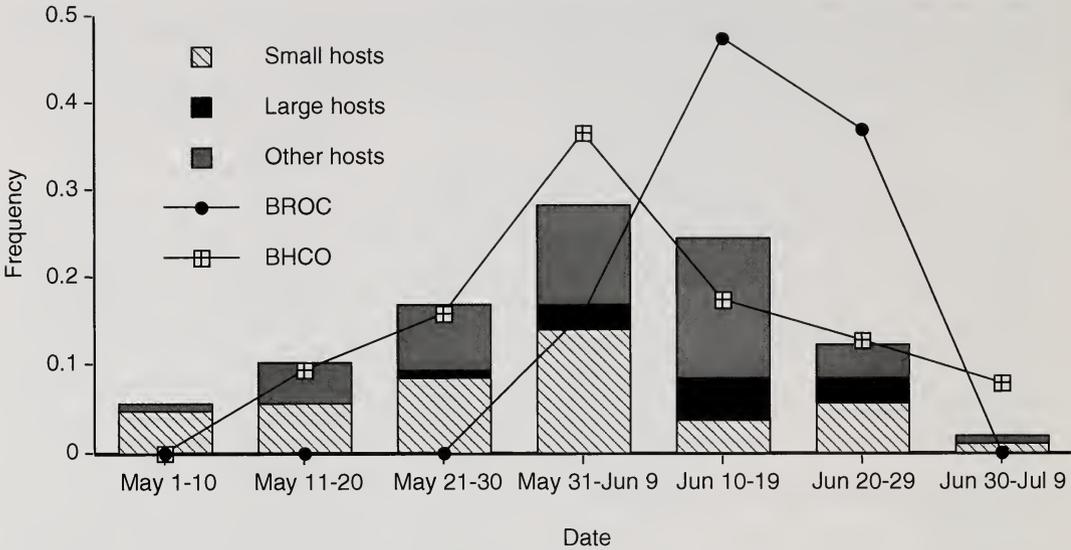


FIG. 1. Host clutch initiation (bars) and cowbird egg laying (lines) in southeastern Arizona, 1997–1999. Brown-headed Cowbirds (BHCO; 41 eggs, 29 nests) laid eggs earlier than Bronzed Cowbirds (BROCO; 21 eggs, 16 nests) ( $d_{\max_{6,62}} = 29.14$ ;  $P < 0.001$ ), coinciding with peak laying of small hosts (<10 g, Bell's Vireo and Painted Redstart). Bronzed Cowbirds laid later than Brown-headed Cowbirds, coinciding with peak laying of larger (38 g, Hepatic Tanager; 28 g, Western Tanager) hosts.

no nests were found, included Virginia's (*Verivora virginiae*), Lucy's (*V. luciae*), Yellow-rumped (*Dendroica coronata*), Black-throated Gray (*D. nigrescens*), and Grace's (*D. graciae*) warblers; Spotted (*Pipilo maculatus*) and Canyon (*P. fuscus*) towhees; Blue Grosbeak (*Passerina caerulea*); Bullock's Oriole (*Icterus bullockii*); House Finch (*Carpodacus mexicanus*); and Lesser Goldfinch (*Carduelis psaltria*).

**Parasitism by habitat.**—Parasitism was significantly higher in the montane riparian forest (57%, 23/41 nests) than pine forest sites (33%, 22/66 nests;  $G_{\text{adj}} = 8.26$ ,  $df = 1$ ,  $P = 0.004$ ). Parasitism frequency within replicate habitats did not differ significantly (pine-oak:  $G_{\text{adj}} = 1.66$ ,  $df = 1$ ,  $P = 0.20$ ; riparian:  $G_{\text{adj}} = 1.71$ ,  $df = 1$ ,  $P = 0.19$ ). In the montane riparian forest sites, Brown-headed Cowbirds parasitized 41% (17/41) of the parasitized nests, whereas Bronzed Cowbirds parasitized 24% (9/41). In the pine-oak forests, Brown-headed Cowbirds parasitized 25% (16/66) and Bronzed Cowbirds parasitized 14% (9/66) of the host nests (NB: three nests in pine-oak forest were parasitized by both species). Bronzed Cowbird parasitism was similar between the two habitat types ( $G_{\text{adj}} = 0.12$ ,  $df = 1$ ,  $P =$

0.73), whereas Brown-headed Cowbird parasitism was higher in the riparian forests ( $G_{\text{adj}} = 8.00$ ,  $df = 1$ ,  $P = 0.005$ ).

**Host-size preference.**—Bronzed Cowbirds parasitized larger hosts than Brown-headed Cowbirds, but both parasitized Hutton's and Plumbeous vireos. Despite this overlap, interspecific parasitism of the same nest was rare, but frequency (0.044) of double parasitism on Plumbeous Vireo nests ( $n = 68$ ) was not different from expected ( $P$  [Bronzed]  $\times$   $P$  [Brown-headed] =  $P$  [Bronzed + Brown-headed] =  $P$  [7/68]  $P$  [22/68] = 0.033;  $\chi^2 = 0.25$ ,  $P = 0.62$ ). Three Plumbeous Vireo nests were parasitized by both parasites. Two of those nests had two Bronzed Cowbird eggs and one Brown-headed Cowbird egg, whereas the third had one egg of each parasite.

**Cowbird laying patterns.**—The peak of cowbird laying was congruent with host clutch initiation, but the Bronzed Cowbird's laying peak was slightly later than that of the Brown-headed Cowbird (Kolmogorov-Smirnov  $d_{\max_{6,62}} = 29.14$ ,  $P < 0.001$ ; Fig. 1). The peak of Bronzed Cowbird laying corresponded with clutch initiation of large hosts (tanagers), while the peak of Brown-headed Cowbird laying corresponded with the peak of

TABLE 2. Number of cowbird eggs found in nests ( $n = 107$ ) of known host species, Huachuca Mountains, Arizona, 1997–1999. Significant departures from the Poisson distribution ( $\chi^2$  goodness-of-fit;  $P^b$ ) and adjusted Poisson (Kolmogorov-Smirnov  $D$ ;  $P^d$ ) suggest nonrandom egg placement by cowbirds among available host nests.

	Number host nests				Total eggs	Mean <sup>a</sup> $\pm$ SD	$P^b$	Mean <sup>c</sup>	$D$	$P^d$
	0 eggs	1 egg	2 eggs	3 eggs						
Brown-headed Cowbird	78	21	4	4	41	1.41 $\pm$ 0.73	<0.001	0.74	7.3	<0.05
Bronzed Cowbird	91	12	3	1	21	1.31 $\pm$ 0.60	0.025	0.57	7.4	<0.01
Both species combined	62	33	7	5	62	1.38 $\pm$ 0.68	0.134	0.68	3.5	>0.50

<sup>a</sup> Mean number of cowbird eggs observed per parasitized nest.

<sup>b</sup>  $\chi^2$  goodness-of-fit test for cowbird egg dispersion versus Poisson distribution.

<sup>c</sup> Mean number of cowbird eggs per nest, calculated across 107 nests available to cowbirds (following Lea and Kattan 1998).

<sup>d</sup> Significance of Kolmogorov-Smirnov  $D$  for test of cowbird egg dispersion versus an adjusted, zero-egg class Poisson distribution.

small hosts (Bell's Vireo and Painted Redstart; Fig. 1).

*Nonrandom egg laying.*—Combined parasitism of both cowbird species was random with respect to the Poisson distribution (Table 2): available host nests were randomly parasitized by at least one of the two cowbird species. Evaluated individually, however, both Bronzed and Brown-headed cowbirds at my study sites laid their eggs nonrandomly among host nests (Table 2), as demonstrated by significant departures from the Poisson. Both the traditional approach (e.g., Elliott 1977) and Lea and Kattan's (1998) more conservative approach yielded the same result (Table 2). Most parasitized nests contained only one parasite egg (range 1–3) and there was no significant difference between the number of Brown-headed and Bronzed cowbird eggs laid per nest (Wilcoxon  $z = 0.68$ ,  $P = 0.75$ ).

## DISCUSSION

In southeastern Arizona, Bronzed Cowbirds typically parasitized larger species than those parasitized by Brown-headed Cowbirds. Both cowbird species dispersed their eggs uniformly with respect to available host nests and generally avoided multiple parasitisms; congruence between the two statistical procedures (typical Poisson and adjusted Poisson distributions) strengthens this assertion. Only Bronzed Cowbirds parasitized tanagers (the two largest host species observed), while only Brown-headed Cowbirds parasitized the two smallest species (Bell's Vireo and Painted Redstarts). Two of three intermediate-sized hosts were parasitized by both cowbird species, but parasitism of the same nest by both cowbird species was rare. My results are con-

sistent with Friedmann's (1967) definition of alloxenia, albeit to a lesser degree than that observed among cuckoos, which, in sympatry, exhibit very low overlap in host use (Brooker and Brooker 1992, Higuchi 1998). An important caveat from my study is that many nests of potential hosts were not found; however, the majority of the nests of the six focal host species were likely found and monitored. My interpretation may have been different had I been able to monitor nests of other species, including those that nest high in the canopy.

Based on the host nests I was able to monitor, my results are not consistent with those indicating that homoxenia occurs among sympatric Bronzed and Brown-headed cowbirds in Texas (Peer and Sealy 1999). Compared with Peer and Sealy's study site in the mesquite grasslands and chaparral of the Texas coastal plains, southeastern Arizona has a greater diversity of hosts, especially smaller, insectivorous passerines. Although not designed as a community study, Peer and Sealy (1999) did not record Bronzed Cowbird parasitism on the smallest host species (Verdin, *Auriparus flaviceps*) in their study area, but they did find extensive overlap in parasitism. Both brood parasites laid eggs in the nests of small- to medium-sized host species (Painted Bunting, *Passerina ciris*; and Olive Sparrow, *Arremonops rufivirgatus*). Surprisingly, Bronzed Cowbirds did not parasitize some of the larger host species (Red-winged Blackbird, *Agelaius phoeniceus*; and Bullock's Oriole) that were parasitized by Brown-headed Cowbirds. No species were found to be parasitized only by Bronzed Cowbirds (Peer and Sealy 1999); however, sample sizes for some of these spe-

cies were very small. Different patterns of host use in southern Texas may have been observed had sample sizes for some of these species been larger (B. D. Peer pers. comm.).

Sympatric cuckoos in Asia, Australia, and Africa, as well as Bronzed and Brown-headed cowbirds reported here, overlap in the use of secondary hosts (Friedmann 1967, Payne and Payne 1967, Brooker and Brooker 1990, 1992; Higuchi 1998). Each of nine species of cuckoos (*Chrysococcyx* spp., *Clamator* spp., *Cuculus* spp.) in southern Africa primarily parasitize one or two hosts of 65 known host species, with only occasional host overlap (Payne and Payne 1967). Australian bronze-cuckoos (*Chrysococcyx* spp.; Brooker and Brooker 1992) and *Cuculus* spp. cuckoos in Japan (Higuchi 1998) are highly host specific in sympatry, but exhibit host overlap when allopatric.

Where parasites overlap in host use, subtle aspects of habitat selection may be involved in segregation (Southern 1954). Differential habitat selection by sympatric brood parasites has been observed among cuckoos (Friedmann 1967, Brooker and Brooker 1992) and cowbirds (Peer and Sealy 1999, Chace 2004). In Africa, three sympatric *Cuculus* spp. cuckoos exhibit a high degree of host specificity as well as habitat specificity (Friedmann 1967). Red-chested Cuckoos (*C. solitarius*) largely parasitize thrushes (*Cossypha* spp.), African Cuckoos (*C. gularis*) parasitize shrikes (*Corvinella* spp.) and drongos (*Dicrurus* spp.), and Black Cuckoos (*C. clamosus*) parasitize boubous (*Laniarius* spp.; Friedmann 1967). To some degree this host partitioning is due to habitat partitioning; Red-chested Cuckoos use the more wooded sites, whereas the African and, especially, Black Cuckoos use relatively open woodlands (Johnsgard 1997). While Bronzed and Brown-headed cowbirds occupied the same four riparian and pine-oak forests in this study, Brown-headed Cowbirds were found across a wider range of habitats than Bronzed Cowbirds (Chace 2004). At broader spatial scales, Bronzed and Brown-headed cowbirds may reduce or avoid competition for host nests through divergent habitat use.

Similar to sympatric cowbirds, sympatric cuckoos overlap extensively in diet, habitat requirements, and use of hosts (Payne and

Payne 1967, Brooker and Brooker 1992). Unlike host-generalist cowbirds, however, cuckoos tend to be host specialists (Davies 2000). Alloxenia is clearly a pattern that is most likely to occur among host and habitat specialists, and it is therefore rather interesting that we find this pattern among generalist cowbirds in Arizona.

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## RESIGHTINGS OF MARKED AMERICAN OYSTERCATCHERS BANDED AS CHICKS

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**ABSTRACT.**—Since 2000, we have been banding American Oystercatcher (*Haematopus palliatus*) chicks at Cape Lookout and Cape Hatteras national seashores as part of a long-term demographic study. Between 2000 and 2002, we banded 23 chicks. We report on resightings of eight chicks that returned to the Outer Banks of North Carolina in the summers of 2003 and 2004. These are the first records of American Oystercatcher chicks resighted near their natal areas in their 2nd and 3rd years. The 3-year-old birds appeared to be paired and acted territorial, whereas the 2nd-year birds were observed alone or in groups and did not exhibit territorial behavior. Our observations suggest that the American Oystercatcher's life history is similar to that of the Eurasian Oystercatcher (*Haematopus ostralegus*). Received 17 November 2004, accepted 1 July 2005.

The American Oystercatcher (*Haematopus palliatus*) is a species of concern (Brown et al. 2001, Davis et al. 2001) that breeds along the eastern coast of the United States (Nol and Humphrey 1994). It is listed in the U.S. Shorebird Conservation Plan as highly imperiled due to habitat loss and because populations are apparently declining in the southeastern U.S. (Brown et al. 2001, Davis et al. 2001). By 1900, the species had been eliminated from regions north of Virginia, primarily due to hunting (Nol and Humphrey 1994). American Oystercatchers have been steadily expanding northward since the 1950s, and the first successful breeding record of oystercatchers in Nova Scotia was in 1997 (Nol and Humphrey 1994, Mawhinney and Benedict 1999, Davis et al. 2001). They are now beginning to occupy new habitats for breeding, such as salt marshes and dredge spoil islands (Frohling 1965, McNair 1988, Humphrey 1990, Toland 1992, Nol and Humphrey 1994, Davis et al. 2001, McGowan et al. 2005). Little is known about dispersal after fledging or about survival in the first 2 years, and these demographic parameters could be important for population viability (Davis 1999). Chicks banded during previous studies in Massachusetts and Virginia (Nol and Humphrey 1994) were never seen after fledging.

As part of a long-term study of oystercatcher demography, we have been banding American Oystercatcher adults and chicks since 2000 at Cape Hatteras and Cape Lookout national seashores in North Carolina (Godfrey and Godfrey 1973). The national seashores are composed of six barrier islands along the North Carolina coast (36° 2' N, 75° 32' W to 34° 35' N, 76° 32' W), including Bodie Island (at the northern end), Hatteras Island, Ocracoke Island, North Core Banks, South Core Banks, and Shackleford Banks (at the southern end). At Cape Lookout National Seashore, a mile-marker system denotes locations within the park; mile 0.0 is located at the northern end of North Core Banks at Ocracoke Inlet.

From 2000 to 2002, we banded 23 chicks between 10 and 25 days after hatching. In 2000, we used federal stainless steel bands and engraved colored aluminum bands to individually mark birds, but the colors faded quickly and we could not identify individual birds without recapturing them. In 2001 and 2002, we marked birds with a federal stainless steel band and a unique combination of colored wrap-around plastic bands. Here, we report on birds banded as chicks that we recaptured or observed in their natal area as 2- and 3-year-olds. These observations were incidental to a separate, long-term study of American Oystercatcher nesting success, and sightings of these birds were recorded opportunistically as we searched for, and checked, nests from ATVs and trucks.

On 4 April 2003, we trapped a territorial adult oystercatcher at mile marker 8.5 on North Core Banks using a noose carpet trap and a decoy (McGowan and Simons 2005).

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This bird was originally banded as a chick on 8 June 2000 on South Core Banks (~25 km to the south). The bird and its presumed mate vigorously defended a territory from a neighboring pair of oystercatchers. The recaptured bird was not seen again during the breeding season and we suspect that it abandoned its territory due to disturbance associated with trapping it.

On 3 June 2003, we observed a 2nd-year bird with three unbanded birds at mile 3.5 on North Core Banks; this bird was originally banded as a chick on 1 July 2001 at Ocracoke Inlet (~5 km away). We observed the same individual again, also with three unbanded birds, on 15 June 2003 at mile 2.4 on North Core Banks. During late May and early June of 2004, this same bird was observed on numerous occasions defending a territory with an unbanded mate near mile marker 4.5 on North Core Banks. On 22 June, it was seen in the same location with a different, banded bird. On 24 June, we observed this bird with three other unbanded birds, and it was no longer exhibiting territorial behavior. We found no evidence of breeding, but its earlier territorial behavior indicated that it might breed on North Core Banks within 1–2 years (Nol and Humphrey 1994, Ens et al. 1996).

During the summer of 2004, we observed six additional 2nd-year birds that were banded as chicks during the summer of 2002 at Cape Lookout and Cape Hatteras national seashores (Table 1). Four of the six birds were seen within 10 km of their hatching site (Table 1). One of those six birds—banded on 11 June 2002 as a chick just north of Buxton Village at Cape Hatteras National Seashore—was observed many times during the winters and summers of 2003 and 2004 at Little Estero Lagoon, near Ft. Myers Beach on the gulf coast of Florida (26° 26' N, 81° 57' W); it was last seen at Little Estero Lagoon on 26 May 2004. On 28 June 2004, that same individual was resighted at Pea Island National Wildlife Refuge, at the northern end of Hatteras Island, and was seen throughout July of 2004 at many locations in the northern part of Hatteras Island.

The 2- and 3-year-old birds that we observed were not breeding. These observations support the notion that American Oystercatchers are long-lived birds with delayed maturation

(Nol and Humphrey 1994), with a life history similar to that of the closely related and extensively studied Eurasian Oystercatcher (*Haematopus ostralegus*; Ens et al. 1996, Bruinzeel 2004). The birds observed as 3-year-olds were apparently attempting to acquire territories and establish pair bonds with a mate. We observed both 3-year-olds exhibiting territorial interactions with other birds, and both were observed with a single other individual (Table 1). None of the 2nd-year birds exhibited territorial behavior or appeared to be paired; rather, they often were seen in groups of three or more birds (Table 1). These 2nd-year birds exhibited behaviors similar to those of subadult Eurasian Oystercatchers that Bruinzeel (2004) called "intruders" or "aggressive club-birds," which move about the breeding grounds alone or in small groups of young birds, gathering information on territory availability and quality. At this point, we cannot report on dispersal distances because we are uncertain whether birds that we observed will return to breed at the locations where we resighted them; however, our observations suggest that American Oystercatchers exhibit strong natal philopatry. Dispersal during the pre-breeding stage probably explains the northward expansion of the American Oystercatcher's breeding range over the last 50 years (Frohling 1965, McNair 1988, Humphrey 1990, Toland 1992, Nol and Humphrey 1994, Mawhinney and Benedict 1999, McGowan et al. 2005). We observed birds moving up to 57 km, and to different islands, from their hatching sites.

Our observations represent the first records of American Oystercatcher chicks to be resighted near their natal territories within 2–3 years of hatching: 34% of the chicks we banded between 2000 and 2002 have been resighted as 2- or 3-year-olds. Although we cannot calculate survival rates on the basis of our opportunistic observations, these relatively high rates of resightings and recaptures bode well for the species and for future analyses of annual survival and dispersal. A better understanding of oystercatcher demography and dispersal is important for safeguarding the future of this species along the eastern coast of the United States (Davis 1999, Davis et al. 2001).

TABLE 1. Original capture dates and locations of eight American Oystercatchers and subsequent capture or resighting dates and locations in North Carolina, 2000–2004. We report national seashore mile markers as reference locations (GPS data were not collected).

Individual	Capture date	Capture location <sup>a</sup>	Recapture date(s)	Recapture location <sup>a</sup>	Distance from initial capture <sup>b</sup>	No. in group <sup>c</sup>
805–60047	6 Aug 2000	South Core Banks	4 Apr 2003	Mile 8.2, North Core Banks	≥25 km	2
805–60059	1 Jul 2001	Mile 0.0, North Core Banks	3 Jun 2003	Mile 3.5, North Core Banks	5.6 km	4
			15 Jun 2003	Mile 2.4, North Core Banks	3.9 km	4
			May–Jun 2004	Mile 4.5, North Core Banks	7.2 km	2
805–60085	1 Jun 2002	Mile 5.9, North Core Banks	28 Sep 2004	Shackleford Banks	57 km	1
805–60088	11 Jun 2002	Buxton, Hatteras Island	28 Jun 2004	Pea Island NWR	42 km	1
805–60091	14 Jun 2002	Ocracoke Island	1 Jul 2004	Mile 6.0, North Core Banks	≥11.2 km	2
			15 Jul 2004	Mile 4.5, North Core Banks	≥8.9 km	2
805–60093	16 Jun 2002	Mile 9.6, North Core Banks	24 Jun 2004	Mile 11.1, North Core Banks	2.4 km	—
			30 Jun 2004	Mile 8.0, North Core Banks	2.6 km	5
805–60100	29 Jun 2002	Mile 9.6, North Core Banks	30 Jun 2004	Mile 8.0, North Core Banks	2.6 km	2
975–85202	1 Jul 2002	Mile 2.3, North Core Banks	10 Jun 2004	Mile 7.0, North Core Banks	7.6 km	3
			11 Jun 2004	Mile 5.0, North Core Banks	4.3 km	—
			22 Jun 2004	Mile 4.5, North Core Banks	3.5 km	4
			24 Jun 2004	Mile 5.5, North Core Banks	5.1 km	—
			1 Jul 2004	Mile 8.0, North Core Banks	9.2 km	3

<sup>a</sup> For some birds, exact locations and mile markers were not recorded; instead, we report the island or general location where captured or resighted.

<sup>b</sup> Approximate distances were calculated using the difference in mile markers and converting to kilometers. Where mile markers were not recorded for captures or recaptures, we report the minimum distance between islands. These distances do not represent dispersal distances, because the breeding or settlement status of these birds is uncertain.

<sup>c</sup> Group size in which each individual was observed. Dashes indicate that no information was recorded.

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## COMPARISON OF WOOD STORK FORAGING SUCCESS AND BEHAVIOR IN SELECTED TIDAL AND NON-TIDAL HABITATS

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**ABSTRACT.**—In 1999, we compared foraging success rates (captures/min) and foraging behaviors of Wood Storks (*Mycteria americana*) at tidal (Georgia) and non-tidal freshwater (South Carolina) foraging sites. Foraging success rates were 30 times greater at the tidal site, but storks foraging in tidal areas only fed at low tide, which limited their foraging time at that site. On-site behaviors indicated the window of prey availability. Storks at the tidal site engaged almost exclusively in foraging behaviors, whereas storks at the non-tidal site devoted more time to other, non-foraging behaviors (e.g., preening, resting). The greater foraging success rate associated with the tidal site suggests that salt marsh/tidal creek habitats are high-quality foraging areas. *Received 21 December 2004, accepted 6 September 2005.*

Wading birds use a diversity of behaviors to acquire prey. Wood Storks (*Mycteria americana*) feed mostly by tactilocation, literally bumping into their prey with partially open bills and capturing prey with a rapid reflex action (Kahl and Peacock 1963). They also employ a repertoire of associated behaviors (e.g., foot stirring, wing flashing) for startling prey or otherwise making them more active and possibly more catchable (Kushlan 1978).

To forage effectively, Wood Storks require shallow wetlands with concentrations of prey (Kahl 1964). Non-tidal freshwater foraging habitats in Georgia are typically shallow, relatively free of vegetation, non-flowing, and support prey densities ranging from 0.1 to 50.0 prey items/m<sup>2</sup> (mean = 7.8 prey/m<sup>2</sup>; Coulter and Bryan 1993). The use of tidal salt marshes by foraging storks has also been documented during both breeding and nonbreeding seasons, and it is presumed that tidal creeks draining as the tide recedes (2.5 m tidal amplitude in Georgia) provide excellent conditions for foraging storks (Gaines et al. 1998, Bryan et al. 2002). To test this presumption, we observed storks within tidal and freshwater non-tidal foraging habitats in 1999 to compare foraging success rates and behaviors. The Wood Stork was federally listed as an endangered species in 1984 due to population de-

clines resulting from loss of their shallow wetland foraging habitats (U.S. Fish and Wildlife Service 1986, 1996). Determining the type and quality of foraging habitat is an important step toward the recovery of this species.

### METHODS

*Study areas and behavioral observations.*—We studied Wood Stork foraging behavior in salt marsh (tidal site) and freshwater (non-tidal site) systems. The 180-ha Purvis Creek salt marsh (tidal site) is located on the western edge of the Brunswick peninsula in Camden County, Georgia (31° 11' N, 81° 31' W). We conducted observations during daylight hours between 6 July and 24 September 1999. The storks included in our observations were non-breeding (postbreeding season) birds. Wood Storks typically forage in the tidal creeks of salt marshes at low tide (Gaines et al. 1998); therefore, we limited our observations to 2 hr before and after dead low tide in tidal creek habitat. We conducted behavioral observations from a camouflaged boat temporarily anchored in an area used by storks. The boat was positioned during high tide and became stranded on the mudflats during our low tide observations. We recorded behaviors of focal storks with a Panasonic VHF video camera. One person (CSE) reviewed all VHF tapes and documented stork behaviors.

We observed foraging storks at a non-tidal freshwater site at the Kathwood ponds in south-central (Aiken County) South Carolina (33° 20' N, 81° 50' W). These 16 ha of freshwater impoundments were established in 1986 and stocked with fish to provide foraging hab-

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itat for storks during the postbreeding season. Coulter et al. (1987) and Bryan et al. (2000) provide detailed descriptions of impoundment management activities. We conducted our observations of storks during crepuscular and daylight hours of July and August 1999, when the impoundments were partially drained to mimic the natural drawdown of freshwater systems. Prey densities in the partially drained impoundments were high relative to natural foraging sites (densities ranged from 10 to 30/m<sup>2</sup>; Bryan et al. 2001). At Kathwood, we used binoculars and spotting scopes to observe storks from a 2-m-tall blind placed at the edge of the impoundments.

We conducted continuous sampling of focal storks (Altmann 1974), which allowed us to calculate time budgets of both foraging and non-foraging behaviors for individual birds. Birds were observed for a minimum of 5 min (Walsh 1990), although longer observations were attempted. Focal storks were observed until they disappeared from view (departed from the site, moved behind an obstruction, or could no longer be distinguished from other storks), at which point we switched to a different focal stork. We recorded the following behaviors while the focal bird was actively foraging: foraging success (captures/min), locomotion patterns (walking with bill out of water, flushing/flying, or standing still), limb movements (foot stirring and wing flashing to enhance foraging), interactions with other birds on the foraging site (aggression), and other general behaviors. We categorized foraging as successful when the focal bird snapped its bill in the water, then raised its bill out of the water (prey were often observed) and tilted its head back as if swallowing. Possible unsuccessful foraging attempts (e.g., bill snapping in the water without subsequently raising the bill) could not be determined with certainty given field conditions (distance and lighting). Stork age (adult, subadult, hatch-year) was determined by plumage characteristics (Coulter et al. 1999).

*Data analysis.*—Specific behaviors during each observation were calculated both on a per-minute basis and as percentages of the total observation period for that bird. We used Wilcoxon rank-sum tests to compare foraging success rates and observation duration of focal storks. Activity patterns and foraging behav-

iors of storks feeding in the tidal site are discussed relative to those of storks in non-tidal sites. Results are presented as means  $\pm$  SD.

## RESULTS

We observed the foraging behaviors of 37 Wood Storks ( $n = 33$  adult, 3 subadult, 1 hatch-year) at the tidal site ( $n = 523$  min total observation time) and 34 Wood Storks ( $n = 14$  adult, 8 subadult, 12 hatch-year) at the non-tidal site ( $n = 2,987$  min total observation time). There were no significant differences in foraging success rates between adult and immature storks at either the tidal ( $Z = 1.05$ ,  $P = 0.29$ ) or the non-tidal ( $Z = 0.84$ ,  $P = 0.40$ ) site; therefore, we pooled the data for adult and immature birds by site. The mean time that focal birds remained and were observable at the tidal site was only  $14.1 \pm 8.6$  min, but was  $87.9 \pm 73.6$  min at the non-tidal site ( $Z = 6.39$ ,  $P < 0.001$ ).

The foraging success rate at the tidal creek site was nearly three prey items captured per min (Table 1). Foraging was by far the most frequent behavior of Wood Storks at the tidal site (Table 1), followed by walking and standing; preening, flying, and aggression combined occupied  $<5\%$  of the birds' time. Behaviors that potentially enhanced foraging efficiency (i.e., foot stirring and wing flashing) were employed at the tidal site.

The foraging success rate at the non-tidal site ( $0.10 \pm 0.09$  prey items/min) was significantly lower than it was at the tidal site (Table 1;  $Z = -6.75$ ,  $P < 0.001$ ). Foraging was also the most frequent activity at the non-tidal site (38% of observation time), with standing and preening being next in importance, together constituting more than half of the birds' activities (Table 1). We did not record observations of foot stirring and wing flashing because documenting these behaviors was not part of the methods used at this site.

## DISCUSSION

The tidal creek system appeared to be a temporally prey-rich foraging habitat for coastal Wood Storks, although there are tide-related time constraints on site use, and prey sizes may be smaller than at non-tidal sites. Storks tended to forage in the tidal creek habitat for shorter periods, but their foraging success rate (2.95 prey items/min) was very high

TABLE 1. Comparison of foraging behaviors (mean per min) and activity patterns (mean percent time) of Wood Storks using tidal (Purvis Creek, Georgia;  $n = 37$  birds) and non-tidal (Kathwood foraging ponds, inland South Carolina;  $n = 34$  birds) habitats in 1999.

	Tidal	Non-tidal
Foraging behavior <sup>a</sup>		
Success rate (captures/min)	2.95 ± 2.42 (0.1–9.6)	0.10 ± 0.09 (0.0–0.46)
Foot stirs/min	8.1 (0.1–17.0)	Not recorded <sup>b</sup>
Wing flashes/min	0.2 (0.0–1.5)	Not recorded <sup>b</sup>
Activity <sup>c</sup>		
Foraging	78.6% (13.7–99.7%)	38.1% (0.1–99.3%)
Standing	10.8% (0.0–31.5%)	32.4% (0.0–81.4%)
Walking	7.6% (0.0–27.1%)	7.3% (0.0–75.0%)
Preening	3.1% (0.0–49.7%)	20.9% (0.0–62.9%)
Flying <sup>d</sup>	0.2% (0.0–0.9%)	1.1% (0.0–12.1%)
Aggression	0.1% (0.0–1.6%)	<1%

<sup>a</sup> Mean ± SD (range).

<sup>b</sup> Documenting these behaviors was not part of the methods used at the non-tidal site.

<sup>c</sup> Mean (range).

<sup>d</sup> Flying indicates movement within the observation area (bird visible throughout movement).

relative to that at the non-tidal site (~30× greater), supporting suggestions that tidal creeks near low tide provide excellent foraging habitat for storks (Gaines et al. 1998, Bryan et al. 2002). Similarly, Grey Herons (*Ardea cinerea*) feeding in Asian tidal sites also had a greater prey-catching rate than those feeding in non-tidal sites (Sawara et al. 1990). Salt-water prey, however, are generally smaller than freshwater prey (Bryan and Gariboldi 1998), and storks likely require more of the smaller prey to meet their energetic needs. Foot stirring was very prevalent (8.1/min) at our tidal site compared with foot stirring in freshwater impoundments in a similar study (0.1/min; Walsh 1990), and may be a more effective strategy within turbid, flowing tidal environments (Kahl 1964).

Wood Storks in tidal habitat spent twice the percentage of time foraging as storks in the non-tidal habitat, possibly due to constraints on prey availability due to tidal cycles. There simply may not have been enough time for storks to spend on non-foraging behaviors during the short period of low tide and prey availability at this tidal site. Storks at the non-tidal site apparently were able to forage at a slower pace, given the longer period of prey availability; thus, they were able to spend more time resting and preening.

Environmental variables at the tidal site also may have affected stork presence. Micro-habitat differences (e.g., creek-bed contour,

depth) among tidal creeks result in suitable depths at different times and for varying durations when the tide is ebbing. Variations in fish abundance and diversity occur daily and seasonally within individual tidal creeks (Cain and Dean 1976, Shenker and Dean 1979, Varnell et al. 1995), which likely affect prey availability in the creek. In addition, the tidal creek site had a narrower field of view than the non-tidal site, and the linearity of the habitat may have limited the length of time focal birds could be kept in view. Finally, disturbances caused some storks to abandon the tidal site. The birds were cognizant of the observer during many of our observations at the tidal site (FCD pers. obs.); on rare occasions, sounds made by the observer within the boat and other boat traffic (from local fishermen) may have resulted in site abandonment by storks.

In conclusion, tidal creeks are important, prey-rich foraging habitats for Wood Storks. Tidal systems are more dynamic than non-tidal systems, with storks having higher foraging efficiencies but shorter periods of prey availability. Storks can move to different tidal creeks within the marsh system, but with associated costs (e.g., travel). In the non-tidal system, capture rates of prey are far lower, but prey items are available for longer periods and are likely larger. It is not known whether the overall mass of prey consumed by individual storks differs between tidal and non-tidal for-

aging habitats. Additional studies of foraging strategies employed by birds using salt marshes (e.g., number of creeks used, total daily foraging time and associated travel time) are needed to determine whether overall consumption rates are similar for the tidal and non-tidal habitats. Regardless, salt marshes are important coastal foraging habitats for postbreeding Wood Storks and should be protected to aid stork recovery.

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## SEXUALLY DIMORPHIC BODY PLUMAGE IN JUVENILE CROSSBILLS

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**ABSTRACT.**—Sexual dimorphism in color and pattern of contour feathers is rare in juvenile songbirds. We describe how captive-bred juvenile males of Scottish Crossbill (*Loxia scotica*) and nominate Red Crossbill (*L. curvirostra curvirostra*) can be differentiated from females prior to prebasic molt by an unstreaked patch on the males' upper breast. There may be a functional relationship between sexual dimorphism and the formation of pair bonds or breeding while the birds are still in juvenile plumage. Sexually dimorphic Red Crossbills and Bearded Tits (*Panurus biarmicus*) are known to form pair bonds, and even breed successfully, while still in juvenile plumage. Received 6 August 2004, accepted 10 July 2005.

Among songbirds, sexual dimorphism in juvenile flight feathers (which are often retained until after the first breeding season) is not unusual, but sexual dimorphism in juvenile contour feathers is rare (Pyle et al. 1987, Svensson 1992). Sexual dimorphism in juvenile crossbills (*Loxia* spp.) has not been reported in the scientific literature (e.g., Svensson 1992, Cramp and Perrins 1994, Adkisson 1996), but, in an unreviewed bulletin for breeders of captive birds (United Kingdom), Castell (1983) reports that juvenile crossbills are sexually dimorphic. Females are described as completely streaked on the underparts, from the base of the lower mandible to the belly. Males differ in that they have a yellowish, unstreaked band or patch at the upper breast, just below the throat (Fig. 1) and an unstreaked chin (but see Fig. 1). In addition, the streaks on the breasts of males are less bold, narrower, and rounder-edged (not square-edged), and the ground color of the breast is a richer color (more yellowish, not whitish). Here, we address the reliability of using the unstreaked breast patch to sex ju-

venile crossbills. We only assessed and report on results pertaining to the breast patch; no quantitative information was available to us for evaluating the reliability of other reported sexually dimorphic traits, although we concur that juvenile males are generally more yellowish in color than juvenile females.

From 1993 to 2003, we tested the validity of using the unstreaked patch to sex 228 juvenile crossbills bred in captivity. All birds were kept in chicken wire and metal-frame aviaries. Adults and chicks were fed with commercial birdseed, supplemented with grit, eggshell or fish bone, and high protein egg feed, and were provisioned regularly with conifer cones. Birds were banded as nestlings with uniquely numbered bands. Pedigrees were known, and most birds were related due to regular inbreeding. The putative and actual sex of each bird was determined by each of three breeders.

Our study entailed sexing juveniles from two different crossbill taxa. The identification of some crossbill taxa can be challenging, and birds in the wild should be identified primarily on the basis of vocalizations, measurements, and geographic location (Groth 1993, Summers et al. 2002, Edelaar et al. 2003). Despite the fact that calls of captive birds are unlike those of wild birds, the (nominate) Red Crossbill (*Loxia curvirostra curvirostra*) is readily distinguished in captivity from other crossbill taxa by bill and body size, as long as the partly overlapping—but typically larger—Scottish Crossbill (*L. scotica*) can be excluded. Our Red Crossbill stock originated from continental Europe (Germany, Austria, and Russia) and had not been crossed with other crossbill

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FIG 1. A juvenile female (left) and male (right) Scottish Crossbill (*Loxia scotica*). Note the continuous streaking across the underparts of the female and the unstreaked patch on the upper breast of the male (upper arrows), and the denser streaking on the underparts (lower arrows) of the female (dark stripes wider than pale stripes) compared with those of the male (pale stripes wider than dark stripes). Contrary to initial reports, however, both sexes seem to have a streaked chin.

taxa. The Scottish Crossbills used in this study were all progeny of wild birds caught in the Scottish Highlands and subsequently isolated from other crossbill taxa during breeding. Our Scottish Crossbill stock has an average bill size thought to correspond closely with that of wild Scottish Crossbills (REP and R. W. Summers unpubl. data), confirming that it did not derive from sympatrically breeding smaller-billed Red and larger-billed Parrot crossbills (*L. pytyopsittacus*).

The putative sex of individuals in juvenile plumage was determined only by the presence (males) or absence (females) of an unstreaked patch on the upper breast, before any juvenile contour feathers had been molted. Actual sex was determined by plumage after prebasic molt. It is known that adult coloration of captive crossbills is dependent on whether many carotenoids are provided during molt (Hill and

Benkman 1995). If carotenoids are not provided, the normally red males develop a yellowish, female-like plumage. On the other hand, unlike many other species, female crossbills in captivity may develop a red plumage when provided with food that is artificially enriched with carotenoids (e.g., Hill and Benkman 1995). Hence, overall color (yellowish or reddish) is of little use when attempting to sex adult birds in captivity. Carotenoid-enriched food was given only to some juveniles (putative males) during the study, but this did not preclude us from correctly sexing all of them after they had undergone prebasic molt. Whether in yellow or red plumage, males have brighter, unmarked feathers on the crown and have a colored (yellow or reddish) chin; females (at least in the taxa we investigated here) have small dark spots on the crown and have a grayish chin

TABLE 1. Reliability of body plumage for sexing captive-bred juvenile crossbills. Putative sex of juveniles was based on the presence (males) or absence (females) of an unstreaked patch on the upper breast and compared to actual sex following prebasic molt. *P* is from a Fisher exact test.

Taxon	<i>n</i>	Males		Females		<i>P</i>
		Putative	Actual	Putative	Actual	
Scottish Crossbill	205	101	99	104	104	<0.001
Red Crossbill	23	8	8	15	15	<0.001

(Phillips 1977, Castell 1983; REP pers. obs.). In offspring kept for subsequent breeding, sex determined on the basis of these adult plumage characteristics was always confirmed by reproductive behavior.

We used Fisher exact tests to determine the correspondence between the putative sex determined by juvenile plumage and the actual sex determined after prebasic molt. A significant *P*-value ( $P < 0.05$ ) indicates that the putative and actual sex correspond better than predicted by chance. We assumed that there were no effects of relatedness, parental care, or rearing environment; we also assumed no differences between observers.

Scottish and Red crossbills were sexed in juvenile plumage with a high degree of reliability (Table 1). Only 2/205 juvenile female Scottish Crossbills were sexed incorrectly ( $P < 0.001$ ), and all 23 Red Crossbills were sexed correctly ( $P < 0.001$ ) in juvenile plumage. We also obtained small sample sizes for Parrot, Himalayan (*L. c. himalayensis*), and Two-barred crossbills (*L. leucoptera bifasciata*). Preliminary information suggests that sexual dimorphism in juvenile plumage of these taxa is not as evident as in Scottish and Red crossbills, as several individuals of both sexes were identified incorrectly as males or females: 6/20 (30%), 2/6 (33%), and 3/7 (43%), respectively. In order to determine the usefulness of plumage dimorphism to sex juvenile crossbills of different taxa, more data on sexual dimorphism in juvenile body plumage should be collected, especially in wild crossbills and for the many Eurasian and North American subspecies of Red Crossbill.

There appears to be a correlation between life history and the occurrence of sexual dimorphism in juvenile body plumage. Juvenile Bearded Tits (*Panurus biarmicus*), which have sexually dimorphic contour feathers, normally form pair bonds, and, like juvenile

Red Crossbills, may even reproduce successfully while still in juvenile plumage (Glutz von Blotzheim and Bauer 1993, Adkisson 1996; K. van Eerde pers. comm., PE pers. obs.). Because reproductive behavior is at least as rare as sexual dimorphism among birds in juvenile plumage, the coincidence of these two traits suggests a possible functional relationship. However, a few other passerine species that exhibit sexual dimorphism in juvenile body plumage (e.g., *Serinus citrinella* [Borras et al. 1993], *S. serinus* [Senar et al. 1998], *Parus major* [Domènech et al. 2000], *P. caeruleus* [Johnsen et al. 2003]) are not known to form pair bonds or breed while in juvenile plumage. Thus, we hypothesize that species that form pair bonds or reproduce while still in juvenile plumage will show sexual dimorphism in juvenile body plumage; the reverse is not necessarily true. For instance, the Red Crossbill subspecies *L. c. tianshanica* is often reported to breed in juvenile plumage (Edelaar et al. 2003); therefore, we predict that juvenile males of this taxon can be distinguished easily from juvenile females on the basis of traits we describe in this paper.

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A DESCRIPTION OF THE NEST AND EGGS OF THE  
PALE-EYED THRUSH (*PLATYCICHLA LEUCOPS*),  
WITH NOTES ON INCUBATION BEHAVIOR

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**ABSTRACT.**—I present a description of the nest, eggs, and nestlings of the Pale-eyed Thrush (*Platycichla leucops*). In addition, I present data on nest temperatures and incubation patterns. Two cup-shaped nests were found at a cloud forest site in the Central Andes of Colombia, both made of moss and containing two greenish-colored eggs with brown blotches. Generally, the incubating female spent the night on the nest. She left the nest at dawn, returned several times during the day and at dusk. Only the female incubated, but the male helped feed the nestlings. Nest temperature varied during incubation between 24° and 27° C, which was several degrees above ambient temperature. There were differences between the two nests in the rate of cooling after the female left the nest at dawn, probably related to nest placement. Nest microclimate was affected by microhabitat and adult incubation behavior. Received 24 January 2005, accepted 28 August 2005.

Thrushes (Turdinae) belong to one of the most widely distributed avian families and occupy a variety of habitats throughout the world (Clement 2000). Although many of the temperate-zone thrush species have been well studied, little is known about thrushes occurring in the New World tropics. There are only two species of *Platycichla*, both of which are restricted to South America, including the island of Trinidad (Ridgley and Tudor 1989, Fjeldså and Krabbe 1990). In contrast, the closely related *Turdus* genus is widespread and species rich (Clement 2000). The two genera are weakly differentiated, leading some authors to suggest that *Platycichla* should be merged with *Turdus* (e.g., Ridgley and Tudor 1989). Mitochondrial DNA sequence data seem to support this suggestion (Klicka et al. 2005).

The Pale-eyed Thrush (*Platycichla leucops*) inhabits montane evergreen forest at elevations of 1,300–2,100 m in the northern and Central Andes and in the tepui region of southern Venezuela and adjacent Guyana and Brazil (Hilty and Brown 1986, Ridgley and Tudor 1989). This species is uncommon and seemingly local in humid montane forest,

where it occurs singly, in pairs, or in groups that congregate at fruiting trees in the forest canopy (Hilty and Brown 1986, Ridgley and Tudor 1989, Fjeldså and Krabbe 1990). For the *Turdus* genus, there is abundant information on incubation and nestling periods, particularly for those species inhabiting the temperate zone. However, this information is lacking for most of the Neotropical species and little is known about the *Platycichla* genus (Hilty and Brown 1986, Ricklefs 1997, Clement 2000).

Here, I describe the nest, eggs, and nestlings of the Pale-eyed Thrush and make relevant comparisons to the well-studied thrushes of the *Turdus* genus. In addition, I describe the nest microclimate and incubation patterns of the Pale-eyed Thrush.

## METHODS

**Study site.**—The study was conducted in the 489-ha Santuario de Fauna y Flora Otún-Quimbaya (4° 43' 11" N, 75° 28' 70" W), on the western slope of the Central Range of the Andes, east of Pereira, Department of Risaralda, Colombia. The area is a mosaic of forest patches (e.g., *Cecropia telealba*, *Siparuna echinata*, *Saurauia brachybotrys*, *Ficus andicola*, *Prestoea acuminata*, *Palicourea angustifolia*, *Miconia acuminifera*) that differ in age—most trees are 40 years or older—and patches are mixed with plantations of Chinese ash (*Fraxinus chinensis*). Small patches of mature, native forest (e.g., *Magnolia hernandezii*, *Ficus killipii*, *Prumnopytis harmsiana*,

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*Juglans neotropica*, *Aniba perutilis*) occur on the ridges (Londoño 1994).

Elevations of the study site range from 1,900 to 2,100 m. Mean maximum and minimum annual temperatures are 20.2° and 11.3° C, respectively. Mean annual rainfall is 2,700 mm and is distributed bimodally; dry seasons (<100 mm rainfall per month) occur December–January and June–August (Ríos et al. 2005).

*Nest monitoring.*—I monitored nests by visiting them at different times in the morning and afternoon. To record patterns of incubation and nest microclimate, I placed a Hobo data logger (Onset Computer Corporation, Bourne, Massachusetts) in each nest. The units had two temperature sensors: one was placed inside the nest cup (at the bottom) and the other was placed outside the nest at the same level as—and 20 cm from—the first sensor. These devices measure temperature with an accuracy of  $\pm 0.36^\circ\text{C}$  with a resolution of  $\pm 0.2^\circ\text{C}$  at  $+20^\circ\text{C}$ . The units were set to record simultaneously the inner and outer nest temperatures every 2 min. During the day, I assumed that females had left their nest to forage if the nest temperature dropped below the range of incubation values known from nocturnal records (when females typically spent all of their time on the nest).

## RESULTS

*Nest description and incubation patterns.*—I report on two nests of the Pale-eyed Thrush. On 15 April 2003, I found the first nest next to a tree-fall gap within a Chinese ash plantation, 35 m from a creek. The nest was 1 m above ground in a 10-cm depression where the three main branches of a live ash (dbh 35 cm) formed a crotch. The nest, built in a clump of epiphytic *Anthurium* sp. (Araceae), was 40 mm deep, had a moss exterior, and an interior lining of black rhizomorph fibers. Because the nest was placed in a tree crotch, the cup was not perfectly round. The nest's inner dimensions were  $96.3 \times 70.0$  mm, the outer dimensions were  $104.6 \times 132.4$  mm, the height was 61.6 mm, and the nest wall averaged 24.7 mm thick. It contained two greenish-colored eggs with brown blotches (concentrated at one end) that varied in shape and density. The eggs differed slightly in size ( $26.1 \times 20.0$  mm and

$27.4 \times 19.4$  mm), but weighed the same (5.25 g).

During the incubation period, 35 observations at different times of day revealed that only the female incubated. Internal temperatures indicated that the female consistently left the nest at dawn (05:30 EST) and returned at dusk (18:00; Fig. 1A). (External nest temperatures were not recorded because the sensor failed.) Nocturnal nest temperatures (when the adult was sitting in the nest) varied between 24° and 27° C. On 18 April, the adult left the nest at approximately 01:00, after which the nest temperature dropped to the lowest recorded ( $\sim 11^\circ\text{C}$ ) during the incubation period. For the next 2 days, the female did not incubate during daylight hours (Fig. 1A). As a result, the general incubation pattern at this nest was highly irregular (Fig. 2A, B). On 22 April, the eggs were depredated. I collected the nest and deposited it in the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN nest collection catalog # ICN-N193).

On 14 May 2003, M. M. Ríos found a second nest 25 m from a creek in mature, native forest. The nest was located in a *Dendropanax macrophyllum* (Araliaceae) tree 1.3 m above ground and inside a 17-cm diameter hole of a broken limb. The nest cup was 64.4 mm deep, and, like the first nest, was not perfectly round because it was constrained by the shape of the hole. The nest's inner dimensions were  $71.1 \times 82.1$  mm, the outer dimensions were  $110.2 \times 130.0$  mm, the height was 81.6 mm, and the nest wall averaged 37.6 mm thick. The nest contained two greenish-colored eggs with brown blotches, resembling those of the first nest. These eggs, however, were slightly larger ( $28.7 \times 20.0$  mm and  $30.6 \times 20.0$  mm), and each weighed 5.5 g. The nest was also constructed of mosses and had a lining of black rhizomorphs. After activating the temperature data logger on 15 May, I left the field site on 20 May and did not return until 2 June, at which time I observed two nestlings in the nest. A substantial temperature increase inside the nest suggested that the eggs hatched late in the afternoon of 27 May (Fig. 1C). On 2 June (day 6 after hatching), the nestlings had yellow down on their heads and backs, their skin was orange, and feather sheaths were emerging on their wings and middle backs.

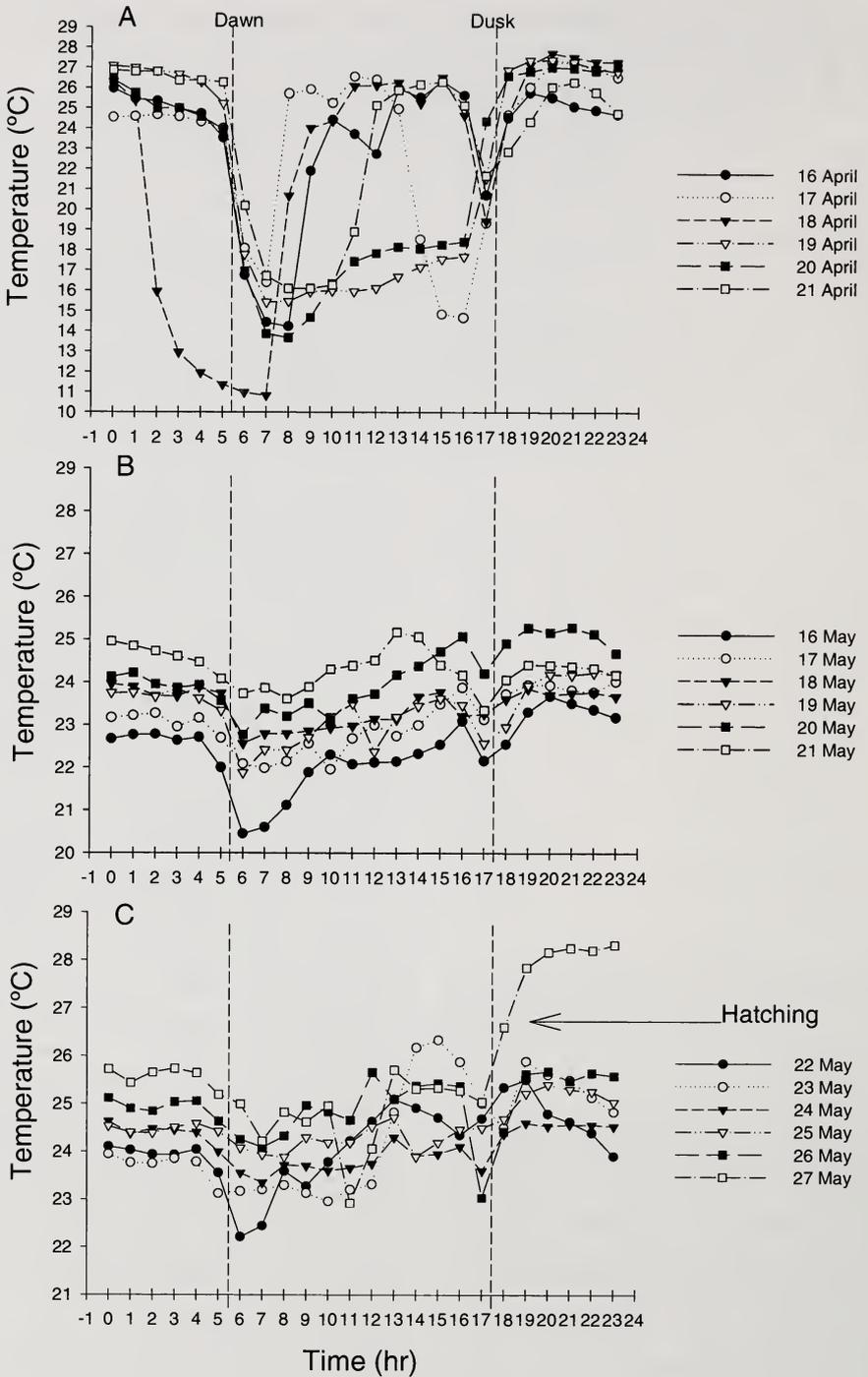


FIG. 1. Mean hourly internal nest temperatures at two Pale-eyed Thrush nests in the Central Andes of Colombia, 2003. (A) Nest 1: 16–21 April; (B) nest 2: 16–21 May; and (C) nest 2: 22–27 May. Temperatures recorded every 2 min during the incubation period with a Hobo Data Logger.

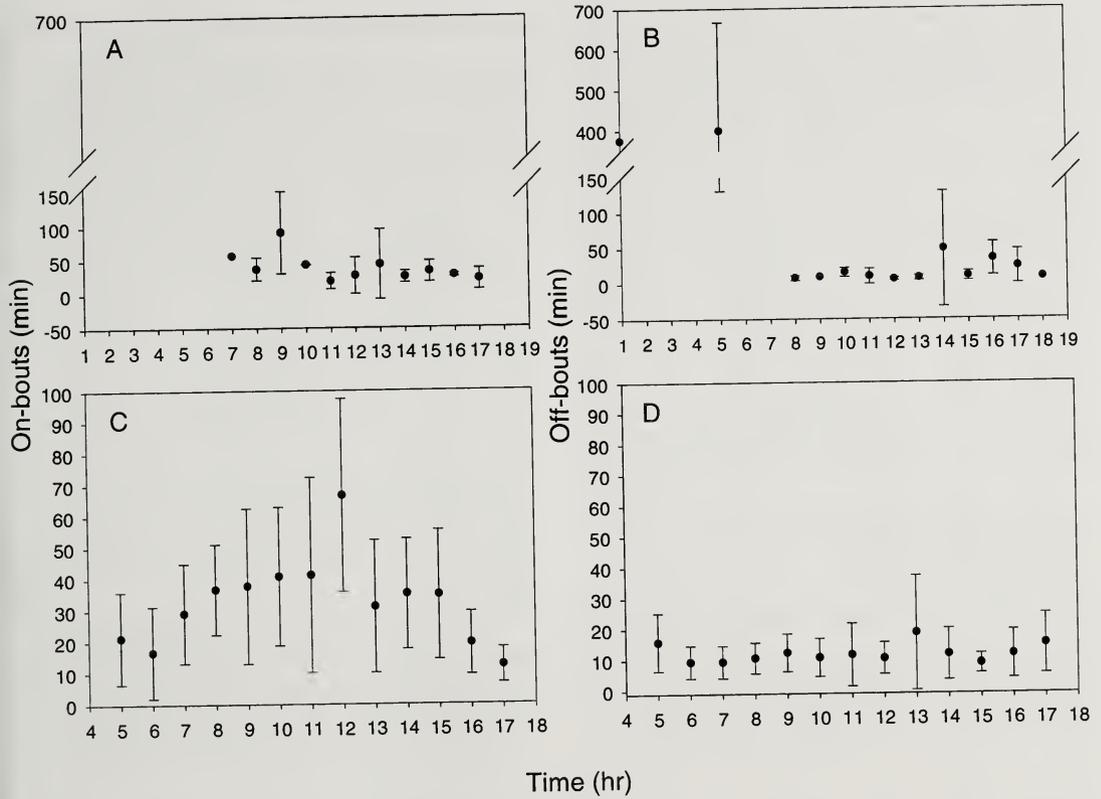


FIG. 2. Female attentiveness at two Pale-eyed Thrush nests in the Central Andes of Colombia, 2003. (A) Nest 1: mean incubation time, 16–21 April; (B) nest 1: mean time spent off the nest, 16–21 April; (C) nest 2: mean incubation time, 16–27 May; (D) nest 2: mean time spent off the nest, 16–27 May. Error bars are  $\pm$  SD.

The nestlings weighed 24.3 and 23.3 g, and their eyes were slightly open. One day later the nestlings weighed 24.5 and 23.8 g, their feather sheaths were longer, and feather sheaths had begun to emerge on their heads. During the nestling stage, both the male and female responded to my presence with noisy alarm calls. I saw both parents feed the nestlings fruits of *Dendropanax macrophyllum*; I later found seeds of this fruit and insect parts in the nestlings' feces. By the morning of 4 June, the nestlings had been depredated. I collected the nest and deposited it in the ICN ornithological collection (catalog # ICN-N194). Photos of the nest, nestlings, and eggs are available at <http://www.zoo.ufl.edu/gustavo/gallery.html>.

Temperature data recorded in the second nest also indicated that the adult left the nest at dawn (05:30) and returned at dusk (18:00; Fig. 1B, C) and that the incubation pattern varied during the day. However, frequent off-

bouts resulted in shorter incubation periods during the early morning and late afternoon compared with those of the first nest (Fig. 2C, D). The longest on-bouts occurred at midday, whereas the longest off-bouts occurred during the next hour (13:00).

### DISCUSSION

The nest of *P. leucops* has been described previously only by Marin and Carrion (1991) and possibly by Goodfellow (1901). Nest shape and egg coloration of the Pale-eyed Thrush were similar to those described by Marin and Carrion (1991) and similar to descriptions for many other species in the thrush family (Hilty and Brown 1986, Ridgely and Tudor 1989, Stiles and Skutch 1989, Clement 2000). However, the nest-site locations of the previously described nests were different from those I describe here; the ones found in Ecuador were located in embankments (Marin and Carrion 1991). The nest of the congeneric

Yellow-legged Thrush (*P. flavipes*) is a shallow cup constructed of roots and mud, lined with moss and fine roots, and typically placed on a bank (Ffrench 1976). Clutch size is two, and eggs are pale blue or greenish-blue marked with reddish-brown (Ffrench 1976). The primary difference in the nests of the two *Platycichla* species is that Pale-eyed Thrushes apparently do not use mud in nest construction. Nest shape, nest materials, and egg coloration of the Pale-eyed Thrush are very similar to those of several species in the *Turdus* genus (Hilty and Brown 1986, Stiles and Skutch 1989, Clement 2000). Nest materials (e.g., moss exterior, black rhizomorphs in the lining), and the nest's low height are similar to those of *Catharus* spp. (*Turdus* nests are usually placed higher than *Catharus* nests; F. G. Stiles pers. comm.).

Typical of thrushes, only the female incubated, but both adults attended nestlings (Clement 2000). Based on the hatching date of the second nest, the Pale-eyed Thrush incubates for at least 13 days. Incubation periods reported for 21 species in the *Turdus* genus average 13 days (range = 11–18 days; Clement 2000); thus, the estimated incubation period of the Pale-eyed Thrush is within the range of *Turdus* spp. There also are no apparent differences in duration of incubation and nestling periods between tropical and temperate species of *Turdus*, although complete information is lacking for all but 2 of the 29 tropical species. As in many species, the clutches of temperate thrushes are larger than those of tropical thrushes (Ricklefs 1997). Because the Pale-eyed Thrush nestlings were depredated, I could not determine the length of their nestling period. It averages 14 days for the *Turdus* genus (range = 9–19 days; Clement 2000).

Nocturnal nest temperatures varied little, due to nearly 100% adult attentiveness. An exception occurred on the night of 18 April, when the female left the nest—possibly to avoid predation—and the nest temperature dropped to 11°C for at least 4 hr. Such behavior can have a strong influence on embryonic development (Turner 2002).

Nest microclimate, and therefore adult behavior at the nest, is determined by a variety of factors, including wind, rain, ambient temperature, nest orientation and shape, clutch

size, and predation risk (Facemire et al. 1990, Sidis et al. 1994, Ghalambor and Martin 2002). Nest microclimate and temperature are probably affected by nest location and materials, especially for open-cup nests (Ar and Sidis 2002, Hansell and Deeming 2002, Hilton et al. 2004). Although I did not measure variables that may have influenced nest microclimate, potential microclimatic differences between nest locations were reflected in the rates of heat loss. These differences were clear when the adult left the nest at dawn: in the first nest the temperature dropped 10–12°C (Fig. 1A), but in the second nest the temperature dropped only 1–2.5°C (Fig. 1B, C). Maintaining nest temperatures during the day can affect the time adults need to spend in bouts of nest attentiveness (Ar and Sidis 2002); in turn, this can affect adult foraging time.

Although descriptions of nests are an important aspect of basic natural history information, they are lacking for many Neotropical bird species. Nest descriptions are crucial for understanding the mechanisms that may drive the high diversity of nest forms and locations, the causes of high predation rates among Neotropical bird species, and the factors that influence nest attendance behavior.

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# Short Communications

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## Interspecific Nest Sharing by Red-breasted Nuthatch and Mountain Chickadee

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**ABSTRACT.**—We report an observation of interspecific nest sharing between Red-breasted Nuthatches (*Sitta canadensis*) and Mountain Chickadees (*Poecile gambeli*) near Williams Lake, British Columbia, Canada. The nest contained two Red-breasted Nuthatch and three Mountain Chickadee nestlings. The nest was attended by a pair of Mountain Chickadees earlier in the observation period and later by an adult female Red-breasted Nuthatch; all five nestlings fledged. Competition for nest sites due to a decrease in cavity availability may have contributed to this occurrence. Received 5 November 2004, accepted 18 July 2005.

The advantage of nesting in cavities is often high success, but cavity nesters must compete with other individuals and species to secure this resource. Competition for cavities can limit population densities where cavity availability is low (Brush 1983, Peterson and Gauthier 1985, Holt and Martin 1997). Red-breasted Nuthatches (*Sitta canadensis*) regularly excavate new cavities; however, they also may reuse or renovate existing cavities. Mountain Chickadees (*Poecile gambeli*) primarily reuse existing cavities, but very infrequently renovate or excavate cavities (KM unpubl. data). Both species are common at our study sites in the Williams Lake area of British Columbia, Canada. The area consists of interior Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) interspersed with patches of grassland and stands of quaking aspen (*Populus tremuloides*; Martin and Eadie 1999). Red-breasted Nuthatches and Mountain Chickadees are resident species that compete for similar nest sites, as both prefer mixed forest with a strong conifer com-

ponent and have similar cavity preferences (Ghalambor and Martin 1999, McCallum et al. 1999, Martin et al. 2004).

Chickadees and nuthatches, along with Downy Woodpeckers (*Picoides pubescens*), comprise a sub-group of small-bodied cavity nesters competing for cavity resources in the nest web (Martin et al. 2004). The rate of extra-group cavity reuse among nuthatches and chickadees is low (17%) relative to the rate of reuse (70%) for primary cavity nesters (Aitken et al. 2002). Thus, high intra-group cavity reuse is the primary source of competition for nest sites among chickadees and nuthatches. If absolute or relative availability of suitable cavities decreased, competition in this group would increase, promoting cavity acquisition strategies, such as usurpation or nest sharing. Steeger and Dulisse (2002) reported increased competition and aggression among cavity nesters in response to changes in the relative abundance of nest sites. Usurpation also occurs in response to decreased nest-site abundance (McCallum et al. 1999). Although not previously reported among Red-breasted Nuthatches and Mountain Chickadees, nest sharing could result from cavity competition if nest initiation by a subordinate pair occurs prior to occupation by a dominant pair, and if the new occupants do not destroy the progeny of the initial pair. In this note, we report a case of interspecific nest sharing, where adults of both species attended the nest, and young of both species were reared to fledging.

### OBSERVATION

In May and June 2004, during the course of our 10-year field investigation of cavity nesters in an area approximately 40 km west of Williams Lake, British Columbia, Canada, we monitored a case of nest sharing involving Mountain Chickadees and Red-breasted Nuthatches (Martin et al. 2004) in a quaking aspen. On 31 May, we observed two adult

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Mountain Chickadees attending the nest and taking insects into the cavity. On 1 June, PAR flushed an adult Mountain Chickadee from the cavity. This was the last detection of adult chickadees at or near the nest. At this time, the cavity was presumed to contain Mountain Chickadee chicks of unknown age. On the next visit (7 June) a female Red-breasted Nuthatch was tending the nest; she entered the cavity with food twice within 5 min. PAR visually inspected the cavity and found five chicks (two nuthatch and three chickadee). On 10 June, the female nuthatch made frequent (approximately once per min) foraging trips from a nearby Douglas-fir tree to the nest. At least two fecal sacs were removed during 6 min of observation. On 11 June, ARN observed all five chicks still in the cavity, and two nuthatch chicks (estimated at 16 days of age) fledged during the observation period. The fledgling nuthatches were seen the next day foraging with the adult nuthatch on and near the nest tree while the cavity still contained three healthy chickadee nestlings. With fewer chicks in the cavity, ARN could see that the nest was lined with fur, typical of chickadee nests, but fresh pitch had been applied to the cavity entrance, which is typical of Red-breasted Nuthatch nests. During this observation, the adult female nuthatch arrived at the cavity without food and vocalized toward the cavity from a nearby branch, apparently encouraging the remaining Mountain Chickadee nestlings to fledge. The female nuthatch then provisioned the chickadee nestlings twice, removing fecal sacs following both visits. On 16 June, the cavity was empty, and with no evidence of predation, we presumed that the chickadees had fledged successfully. Because no birds were banded, subsequent sightings of Red-breasted Nuthatches or Mountain Chickadees in the area could not be associated with this nest.

The study plot where the observation occurred was in a 26-ha stand of mixed deciduous and coniferous forest consisting of 85% Douglas-fir, 4% lodgepole pine, 8% spruce (*Picea* spp.), and 3% quaking aspen. In 2002, we found four Red-breasted Nuthatch nests, and in 2003, we found one nuthatch and five Mountain Chickadee nests. The study plot was selectively harvested in the fall of 2003. The nest tree (recently dead aspen, 30.2 cm dbh)

was situated at the edge of the cutblock. In 2004, the first post-cut year, we monitored two Red-breasted Nuthatch and two Mountain Chickadee nests in addition to the shared nest cavity. This was our only observation of interspecific nest sharing and brood rearing in our 10-year study of cavity nesters, during which we monitored 691 nests of small cavity nesters (52 Black-capped Chickadee, *Poecile atricapillus*; 42 Downy Woodpecker; 340 Mountain Chickadee; and 257 Red-breasted Nuthatch).

## DISCUSSION

Although active competition—in the form of aggression before clutch initiation and nest usurpation before and during incubation—is frequently reported (Ghalambor and Martin 1999, McCallum et al. 1999), this is the first record of Mountain Chickadees and Red-breasted Nuthatches successfully rearing their young in a nest attended by both parental species. In our study area, nuthatch nest density more than tripled from 0.03 nests/ha during 1996–2000 to 0.10 nest/ha during 2001–2004; during the same period, chickadee nest density increased from 0.05 to 0.14 nests/ha (KM unpubl. data). This may be a result of regional changes in tree condition and an increased abundance of forest insects (KM unpubl. data). Nuthatches and chickadees prefer dead and decaying aspen trees, which composed <7% of trees on our stands (Martin et al. 2004). Furthermore, nest-site availability decreased at a local scale, due to cutting on the site. Thus, both the absolute and relative availability of nest sites decreased in our study area. These factors, combined with the recent tripling of nuthatch and chickadee populations, may have increased encounter rates and interspecific competition, facilitating the nest-sharing occurrence.

We were able to confirm nest sharing because we visited the nest tree and inspected the cavity visually on multiple occasions. Unfortunately, we did not locate this nest until after the eggs had hatched; thus, we could not determine the circumstances during clutch initiation and incubation. We suspect that Mountain Chickadees initiated the nest because the cavity was lined with fur. In addition, Mountain Chickadees consistently fledge in 21 days (McCallum et al. 1999), whereas Red-breasted

Nuthatches remain in the nest anywhere from 14 to 21 days (Ghalambor and Martin 1999); therefore, the nuthatches could have fledged before the chickadees, even if the nuthatch eggs were laid after the chickadee eggs. Last, we did not observe a male nuthatch at the nest. Given the aggressive nature of male nuthatches and the fact that nuthatch pairs can out-compete Mountain Chickadee pairs (ARN unpubl. data), we suspect the absence of a male nuthatch was an important contributing factor in this occurrence of interspecific nest sharing.

Others have reported interspecific nest sharing where two species laid eggs in the same nest, and in some cases, successfully fledged broods because of cooperative incubation and feeding of nestlings (Skutch 1961, Sundkvist 1979). In Norrbotten, Sweden, a pair of Pied Flycatchers (*Ficedula hypoleuca*) and a female Common Redstart (*Phoenicurus phoenicurus*) shared a nest box and successfully reared the young of both species, despite aggressive encounters between the species during incubation (Sundkvist 1979).

Variation in timing of breeding and dominance can result in cross-species broods. Cavity-nesting Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*) regularly produce cross-species broods when the earlier-nesting, socially subordinate Blue Tits initiate clutches that are subsequently usurped by the later-nesting, but dominant, Great Tits (Slagsvold 1998). Our nest-sharing observation had some similarities to the tit example, as Mountain Chickadees are subordinate to nuthatches but tend to initiate clutches about 3 days earlier (KM, ARN unpubl. data). Because chickadees do not readily defend their territories against intrusions by nuthatches (ARN unpubl. data), the female nuthatch may not have been deterred by territorial behavior of the chickadee pair.

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## Nelson's Sharp-tailed Sparrow Nest Parasitized by Brown-headed Cowbird

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**ABSTRACT.**—On 22 July 2004, we found a Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*) nest in Sheridan County, Montana, containing a single Brown-headed Cowbird (*Molothrus ater*) nestling that was about to fledge. A punctured sharp-tailed sparrow egg was found below the nest. This is the second definitive report of cowbird brood parasitism of a Nelson's Sharp-tailed Sparrow nest and the first indicating successful rearing of a cowbird by this host species. The impact of cowbird parasitism on nesting success of Nelson's Sharp-tailed Sparrow has not been studied, but our record indicates that nest failure (i.e., producing no host young) may be an outcome for some nests of this species. Received 18 January 2005, accepted 10 August 2005.

During an inventory of wetland-associated bird species in northeastern Montana, we surveyed wetlands on McCoy Creek, Sheridan County (48° 49' 57" N, 104° 35' 36" W), in June and July 2004 to observe the activities of singing grassland sparrows found there. On 19 July, TJN and MPN saw a pair of Nelson's Sharp-tailed Sparrows (*Ammodramus nelsoni*) carrying food four times and fecal sacs three times during 75 min of observation, but could not find the nest. On 22 July, TJN and MPN found the nest after watching the adults make two feeding trips to the same general area.

The nest was in dense wetland vegetation of sedges (*Carex* spp.), rushes (*Scirpus* spp.), and unidentified grasses about 100 cm tall; the nest rim was 23 cm above ground. The nest was built of coarse grass and lined with finer grasses; inside cup dimensions were 3.5 cm deep and 5.0 cm in diameter, typical for nests of this species (Greenlaw and Rising 1994). The nest contained a single Brown-headed Cowbird (*Molothrus ater*) nestling that filled

the entire nest cup. The cowbird was well feathered, with sheathing present on the proximal two-thirds of the primaries; we estimated that it was about 8 days old, or within a few days of fledging (Scott 1979). We photographed and videotaped the nest contents and surrounding area and deposited digital copies with the Montana Natural Heritage Program in Helena.

On 24 July, we revisited the nest and found it empty. We assumed the cowbird nestling had fledged, but neither saw nor heard the sparrows or the cowbird during 30 min of observation. We found a single, punctured sharp-tailed sparrow egg on the ground below the nest that had been overlooked on the day the nest was discovered. The egg measured 17.5 × 14.2 mm, was bluish-white in color, and was covered with numerous fine, light-brown maculations—typical in size, coloration, and markings for Nelson's Sharp-tailed Sparrow, although slightly shorter than average (Greenlaw and Rising 1994). The eggs and nest of Le Conte's Sparrow (*A. leconteii*) are similar (Lowther 1996) to those of Nelson's Sharp-tailed Sparrow, and, in northeastern Montana wetlands, Le Conte's Sparrow is sympatric with Nelson's Sharp-tailed Sparrow (PH pers. obs.); however, we neither saw nor heard any Le Conte's Sparrows at this site on any of our five visits. Thus, we are confident that the nest and egg belonged to the pair of Nelson's Sharp-tailed Sparrows we observed near the nest site. The nest and punctured egg were collected and deposited in the Philip L. Wright Zoological Museum at the University of Montana, Missoula (UMZM 18620).

Our observation of cowbird brood parasitism on Nelson's Sharp-tailed Sparrow is significant for several reasons. First, it is only the second definitive record of a cowbird parasitizing this host species. The first was of a single cowbird egg found in a clutch of four sharp-tailed sparrow eggs near Brandon, Man-

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itoba, on 20 June 1962 (Hill 1968). In his comprehensive summary of host species, Friedmann (1963) listed an earlier, third-party recollection of an associate who found a Nelson's Sharp-tailed Sparrow nest containing a cowbird egg, but no additional details regarding date or location were provided; thus, the record is hypothetical. Second, our report is the first to confirm that this species can successfully rear a cowbird nestling (Friedmann and Kiff 1985, Greenlaw and Rising 1994, Shaffer et al. 2003). Third, our observation indicates that nest failure (i.e., producing no host young) is a possible outcome when cowbirds parasitize Nelson's Sharp-tailed Sparrow, perhaps resulting in reproductive failure for an entire breeding season.

Nelson's Sharp-tailed Sparrow is arguably among the most poorly known of North American sparrows. In particular, very little information is available on this species' nesting ecology or its habitat requirements in the northern prairie states and provinces (Greenlaw and Rising 1994) because the nests are notoriously difficult to locate. Therefore, the impact of parasitism by Brown-headed Cowbirds on populations of Nelson's Sharp-tailed Sparrow in the northern Great Plains is unknown. Friedmann (1963) was probably overly optimistic in concluding that the nesting habitat used by Nelson's Sharp-tailed Sparrow would buffer it from significant cowbird parasitism. On a small North Dakota site occupied by both Le Conte's and Nelson's Sharp-tailed sparrows (Murray 1969), all five Le Conte's Sparrow nests found were parasitized, indicating that cowbirds were active in the habitat where sharp-tailed sparrows nested. Studies of additional Nelson's Sharp-tailed

Sparrow nests may prove that cowbird parasitism is more frequent than evidence currently indicates.

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## Dunking Behavior in American Crows

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**ABSTRACT.**—Dunking behavior, the immersion of food items in water, is a relatively rare behavior in birds. I observed American Crows (*Corvus brachyrhynchos*) dunking several types of food in rain puddles at Mont-Royal Park, Montréal, Québec, Canada. Pieces of dry bread and unshelled peanuts were provided in two experiments to test the potential effects of item size (bread) and shell softening (peanuts) on crow behavior. Crows dunked large pieces of bread more often than small ones. Dunking unshelled peanuts did not speed up the opening process. These observations further support the suggestion that food dunking among birds facilitates food ingestion by softening large, hard items. Received 3 November 2004, accepted 11 July 2005.

Dunking behavior, the immersion of food items in water, is a relatively rare behavior in free-ranging birds; fewer than 40 species have been reported dunking food (Morand-Ferron et al. 2004). Prevalent among these records are members of the genera *Quiscalus* (5 species out of 6) and *Corvus* (7 species out of 43). In this paper, I describe dunking behavior in another corvid species, *Corvus brachyrhynchos*. Although well known among naturalists (C. Caffrey pers. obs.), dunking behavior in American Crows has not been reported in the literature. Reports of unusual behaviors are useful in estimating the taxonomic distribution of innovative behaviors, which can be used to test predictions in neurobiology, ecology, evolution, and cognition (Reader and Laland 2003).

On 21 September 2003, at 11:00 EST, I observed a single crow pick up two pieces of dry white bread (3 × 3 cm) that had been thrown on the ground near the entrance of the Lac-aux-Castors section of Mont-Royal Park in Montreal, Quebec, Canada. The bird then flew to a nearby (10 m) rain puddle and dunked the food in it twice before eating it on

the spot. On 23 September, I returned to the park and again witnessed a free-ranging crow dunking bread. Between 23 September and 16 October, I observed at least three different individuals (birds were not marked, but sometimes they dunked almost simultaneously in different puddles) dunking fresh and dry bread and unshelled peanuts. I also observed crows eating dry dog food pellets ( $n = 16$ ), maraschino cherries ( $n = 2$ ), and live crickets ( $n = 6$ ) that I placed 8 m from the nearest rain puddle; however, I observed no crows dunking these items (all previously reported as dunked by other species; see table in Morand-Ferron et al. 2004).

From these observations alone, it is difficult to determine the function of dunking behavior in wild American Crows. Among the different functions suggested for this behavior in birds, using food as a sponge for bringing water to nestlings (Koenig 1985) can be ruled out because the events I observed occurred many weeks after juveniles had fledged. Washing soiled food (Simmons 1950, Watkin 1950, Caldwell 1951, Jordheim 1965, Wible 1975, Johnson 1976, Seibt and Wickler 1978, Vader 1979, Zach 1979, Schardien and Jackson 1982, del Hoyo et al. 1996, Henry et al. 1998) also may be ruled out because the food items were soiled during the process of dunking clean food into muddy rainwater.

I conducted two field experiments with bread and peanuts to examine two possible determinants of dunking: the effect of item size on the dunking frequency of bread and the advantage that dunking might offer in softening peanut shells (making them easier to open). In the first set of trials, I tested the hypothesis that dunking hard food would be more prevalent with larger items (too large to be swallowed whole) than with smaller items. I provided crows ( $n = 3$ ) at Mont-Royal Park with two sizes of dry bread: small (2 × 2 cm,  $n = 16$ ) and large (4 × 4 cm,  $n = 17$ ). I ran one trial per day between 10:00 and 12:00 on

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4 days in October 2003. During each trial, I recorded the behavior of crows provided with 6 to 10 pieces of bread. One piece at a time, I threw bread on the ground, alternating between the two sizes each time. I noted whether the crow that took the piece dunked it in a nearby puddle (8 m away) or ate it dry. A chi-square test revealed that the large pieces were dunked more often than the small ones (58.8 versus 18.8% respectively;  $\chi^2 = 5.53$ ,  $df = 1$ ,  $P = 0.014$ ). This result suggests that the size of food items might influence the frequency of dunking behavior in birds.

In the second set of trials, I tested the hypothesis that crows dunking peanuts could accelerate the shelling process by softening the shell in water. The potential advantage of reduced handling time, however, needs to be distinguished from the possibility that dunking peanuts lubricates them and allows the bird to swallow them whole. I observed the latter behavior once in Ring-billed Gulls (*Larus delawarensis*)—which also have been reported dunking crackers (Stokes and Stokes 1985)—but not in crows. From 10:00 to 12:00 on 4 days between 26 September and 16 October 2004 and on 4 days between 7 and 14 April 2005 ( $n = 5$  trials in 2004 and  $n = 6$  in 2005), I provided crows with unshelled peanuts near a rain puddle (8 m away) at Mont-Royal Park. On each day, I made a similar number of observations on peanuts that crows dunked and did not dunk ( $n = 4$ –8 peanuts per day). I defined shelling latency as the time it took to access the second peanut inside a two-peanut shell, not including the time spent in locomotion. I discarded observations where the crow did not eat the second peanut but cached it in the grass ( $n = 3$ ). On average, shelling latency was  $55.1 \text{ sec} \pm 35.7 \text{ SD}$  when the crows dunked ( $n = 22$ ) and  $65.4 \pm 48.6 \text{ sec}$  when crows did not dunk the peanuts ( $n = 26$ ;  $t = 0.818$ ,  $df = 46$ ,  $P = 0.42$ ); thus, dunking did not accelerate the peanut-shelling process. After extracting them from the shell, crows sometimes dunked peanut halves in water, which resulted in removal of the peanut skin. This behavior has also been observed in Common Grackles (*Quiscalus quiscula*; Wible 1975).

The function of dunking behavior seems to vary depending on the species performing it and the item dunked. For example, raptors kill

live prey by holding it under water (e.g., *Accipiter nisus*; Weekley 1997). Shorebirds are thought to wash muddy items by rinsing them in water before consumption (e.g., *Tringa hypoleucos*; Simmons 1950). Studies on Carib Grackles (*Quiscalus lugubris*) have revealed that birds dunk dry bread more often than fresh bread (Morand-Ferron et al. 2004) and that dunking hard items reduces handling time (JM-F unpubl. data); these results suggest that food dunking among Carib Grackles is a food-processing technique to facilitate the ingestion of items that otherwise would be difficult to swallow. My observations on American Crows dunking bread suggest a similar function. A peculiarity of corvid dunking behavior seems to be its variability: observations indicate that dunking is used to transport water to nestlings (*Corvus corax*; Hauri 1956), drown live prey (e.g., *Pica nuttalli*; Blackburn 1968), wash soiled items (e.g., *Corvus caurinus*; Zach 1979), and soften hard (*Corvus corone*; Goodwin 1986) or large items (*Corvus brachyrhynchos*; this study). My observations add to the diversity of dunking behaviors reported for corvids and further support Goodwin's (1986) suggestion that dunking may be a standard part of the feeding repertoire in the genus *Corvus*.

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## An Apparent Case of Cooperative Hunting in Immature Northern Shrikes

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**ABSTRACT.**—Cooperative hunting is a behavior rarely observed in passerine birds. I observed two immature Northern Shrikes (*Lanius excubitor invictus*) apparently hunting cooperatively while preying on American Tree Sparrows (*Spizella arborea*) in central Alaska. During each of three foraging attempts, both shrikes appeared to work together to flush prey from dense cover into the open where it was then pursued. Cooperative hunting in this otherwise solitary species may be an adaptive behavior among inexperienced birds to increase their foraging efficiency, or to compensate for seasonal fluctuations in the accessibility or availability of prey. *Received 6 December 2004, accepted 9 July 2005.*

Many raptorial birds are considered solitary predators (Schoener 1969); however, more social forms of foraging may be adaptive if the outcome results in increased foraging efficiency or compensates for fluctuations in prey populations (Packer and Ruttan 1988, Ellis et al. 1993). Cooperative hunting in mammals has been extensively documented in large, social carnivores (Packer and Ruttan 1988) and some diurnal raptors (Hector 1986, Bednarz

1988, Yosef 1991). Only rarely, however, has social foraging been reported in passerine birds (see Bowman 2003). Generally, social foraging is not thought to be a common foraging strategy within the genus *Lanius*, although a case of cooperative hunting was observed in mated Loggerhead Shrikes (*Lanius ludovicianus*; Frye and Gerhardt 2001). In this paper, I report an apparent case of cooperative hunting by immature Northern Shrikes (*Lanius excubitor invictus*).

The observation took place in Denali National Park, Alaska (63° 44' N, 149° 22' W) between km 28.1 and 28.8 of Denali Park Road, near a small tributary creek of the Savage River. Vegetation at the site was primarily riparian, with many species of willow (*Salix* spp.) ranging in height from 1 to 5 m, contrasting markedly with the surrounding vegetation. Vegetation in the surrounding area was characteristic of the taiga/tundra interface, consisting of widely spaced, stunted 1- to 5-m-tall white spruce trees (*Picea glauca*); dwarf birch (*Betula glandulosa*), willow (*Salix* spp.), and blueberry (*Vaccinium uliginosum*) were the dominant cover species. Elevation at the site was approximately 880 m, with marked topographical relief in the surrounding area. Ambient temperature at the time of the observation was  $-4^{\circ}\text{C}$ .

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While driving along the Denali Park Road on 19 September 2003, I noticed two Northern Shrikes perched in close proximity to one another. I observed and photographed both birds from  $\leq 12$  m and identified them as immature birds—based on the fine dusky vermiculations on their underparts, an overall brownish appearance, and grayish-brown supercilia (Cade and Atkinson 2002). As I exited my vehicle at 10:30 AST, both birds flew approximately 50 m and perched approximately 20 m apart in a thick patch of willows 3–5 m in height. Both birds then flew into the willow thicket, where I could see them sporadically as they hopped along branches.

Suddenly, one of the shrikes flew up out of the thicket, chasing an American Tree Sparrow (*Spizella arborea*). The shrike pursued the sparrow upward, making quick, horizontal lunges at the sparrow as it continued to ascend. After 5–6 sec, the shrike and the sparrow reached an altitude of approximately 30 m above the ground. At this point, the second shrike joined in the pursuit, with both shrikes alternately making horizontal lunges at the sparrow. After an additional 8–10 sec, the sparrow made a quick vertical descent to a willow thicket. The shrikes discontinued their pursuit of the sparrow and flew back to the original willow thicket, where they perched several meters apart near the top.

One of the shrikes then began to sing irregularly, uttering a series of trills and warbles as described by Cade and Atkinson (2002). After approximately 2 min, both birds flew into the willow thicket. At about 10:45, one shrike emerged from the willow thicket, chasing an American Tree Sparrow upward in much the same manner as in the previous chase. Within 5–6 sec, the second shrike joined in the pursuit. Following several alternating horizontal lunges by the shrikes, the sparrow made a quick vertical descent and flew into dense vegetation. The two shrikes returned to the original willow thicket and flew back into cover. At 10:50, another American Tree Sparrow—pursued by both shrikes—flew up out of the thicket. In contrast to the first two pursuits, all three birds reached an altitude of  $\sim 45$ –50 m above the ground, and both shrikes made 10–15 horizontal lunges at the sparrow. The sparrow, which showed signs of fatigue, began a slightly more horizontal descent than

the one made during the previous two chases. One of the shrikes then began a direct pursuit of the sparrow, which was flying almost completely horizontally. After pursuing the sparrow for  $\sim 8$ –10 sec, covering a distance of approximately 150 m, the shrike captured the sparrow by grasping it with its bill and quickly transferring the prey to its feet. The shrike then flew to a large willow, perched, and bit the sparrow's head and neck, apparently killing it.

At this point, the second shrike flew in, perched  $\sim 5$  m away from the first shrike, and uttered a loud “waik” call (Cade and Atkinson 2002). The first shrike, responding with a similar call, flew approximately 120 m to the east and perched at the top of a small spruce. The second shrike pursued the first shrike, perching nearby and again uttering the waik call. Grasping the sparrow with its feet, the first shrike flew  $\sim 400$ –500 m farther before disappearing over a ridge, with the second shrike in pursuit. Thereafter, I was unable to refind the birds; thus, I could not determine whether the prey item was shared.

Although little is known about the diet of Northern Shrikes during autumn migration, passerine birds are thought to represent only a minor portion of the summer and winter diet, in both number and biomass (Cade 1967, Atkinson and Cade 1993). Compared with other prey taxa, Northern Shrikes have very low foraging success when hunting birds (Cade and Atkinson 2002), often taking them by surprise and only rarely in flight (Cade 1967). Although insects constitute a large proportion of the Northern Shrike's diet (Atkinson and Cade 1993), the extremely cold autumn temperatures in this region would likely reduce their availability as potential prey. Access to small mammals—another significant part of the shrike's diet—might be limited in dense, shrubby habitat such as that along Denali Park Road. Therefore, small flocks of migrating passerines may represent an opportunistic, albeit highly important food source for shrikes migrating through this area in late autumn. By hunting cooperatively, inexperienced shrikes may overwhelm or surprise elusive prey, thereby reducing the potential for escape and increasing hunting success. Consequently, social foraging may be adaptive, by increasing the foraging efficiency on this

highly elusive, though seasonally abundant food resource.

According to Ellis et al. (1993), my observation may represent true cooperative hunting—a form known as sibling group hunting, wherein two or more sibling fledglings hunt cooperatively. Although I could not determine whether these birds were siblings, small groups of immature shrikes during the early part of autumn migration are thought to consist of siblings (Cade and Atkinson 2002). Whereas true cooperative hunting has never before been reported in the Northern Shrike, cooperative hunting by sibling groups may be an adaptive strategy used by younger, less experienced raptorial birds to improve hunting efficiency (Packer and Ruttan 1988, Ellis et al. 1993). As individual birds develop their hunting skills and increase their foraging efficiency, the need to hunt cooperatively probably declines (Bosakowski and Smith 1996, Brown et al. 2004). Alternatively, as shrikes migrate farther south, other prey taxa may once again become more available and accessible, resulting in a smaller proportion of birds in their diet and fewer instances of social foraging. Generally, previous accounts of cooperative hunting in passerines, such as Common Raven (*Corvus corax*; Hendricks and Schlang 1998), Loggerhead Shrike (Frye and Gerhardt 2001), and Florida Scrub-Jay (*Aphelocoma coerulescens*; Bowman 2003), have involved mated adult pairs cooperatively hunting large or dangerous prey. My observation is novel in that it involved immature passerines cooperatively hunting smaller prey. Further study is required to determine the frequency and adaptive significance of social foraging in passerine birds.

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## A Field Observation of the Head-down Display in the Bronzed Cowbird

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**ABSTRACT.**—We describe a photodocumented field observation in Sinaloa, Mexico, of a head-down (or “preening invitation”) display performed by a male Bronzed Cowbird (*Molothrus aeneus*), which elicited both grooming and pecking responses from a female Great-tailed Grackle (*Quiscalus mexicanus*). Previously, such displays by parasitic cowbirds and responses by conspecific or various heterospecific bird species have been documented mainly under aviary conditions; most field observations have involved Brown-headed (*M. ater*) and Shiny (*M. bonariensis*) cowbirds. The function and evolutionary significance of such interspecific interactions remain elusive, but continued documentation of such occurrences may help elucidate their biological significance. Received 10 December 2004, accepted 2 August 2005.

On 17 December 2003 at 08:15 MST, we observed a mixed group of icterids, including 40 Great-tailed Grackles (*Quiscalus mexicanus*), 20 Bronzed Cowbirds (*Molothrus aeneus*), and 1 Brown-headed Cowbird (*M. ater*), in several small palo verde (*Cercidium* spp.) trees along the southern shoreline of the Eustaquio Balbuena reservoir in Guamuchil, Sinaloa (25° 28' N, 108° 06' W). Among these birds was a male Bronzed Cowbird giving a head-down display with its neck ruff flared out, matching the “interspecific preening invitation display” described by Selander and La Rue (1961). The bird remained very still in this position for most of our 5-min observation. A female Great-tailed Grackle spent several minutes within 5–15 cm of the cowbird, lateral to and slightly below it, gently picking at the cowbird’s head about eight times. The grackle also delivered six slightly stronger pecks toward the Bronzed Cowbird, but did not cause the cowbird to move from its perch. At the end of this interaction, the cowbird shifted upward along the branch to a position about 30 cm from the grackle. We

could not determine whether the grackle was obtaining food items—such as ectoparasites—from the cowbird, but its bill motion was clearly that of gentle picking rather than preening through the feathers. KCM photographed the display (a series of eight digital images) under clear conditions at 15° C with a very light breeze (Fig. 1).

It appears that head-down displays directed by cowbirds toward—and eliciting responses from—much larger grackles are not common. Selander and La Rue (1961) described interspecific preening invitation displays by Brown-headed Cowbirds in captive, mixed-species flocks and briefly mentioned a similar display performed by two captive Bronzed Cowbirds; these authors noted brief displays by Brown-headed Cowbirds toward female Great-tailed Grackles, which elicited no responses from the grackles. Selander (1964) recorded additional such displays to heterospecifics by captive Shiny (*M. bonariensis*) and Bay-winged cowbirds (*Agelaioides [Molothrus] badius*). Such preening invitation, or head-down (Rothstein 1977), displays are now well documented in wild Brown-headed Cowbirds (Selander and La Rue 1961, Dow 1968, Rothstein 1977, Lowther and Rothstein 1980, Hunter 1994) and in captive (Harrison 1963) and wild (Chapman 1928, Payne 1969) Giant Cowbirds (*M. oryzivorus*). Post and Wiley (1992) observed Shiny Cowbirds in the field directing 33 of 238 head-down displays toward Greater Antillean Grackles (*Q. niger*). Rothstein (1977) has also documented these head-down displays among conspecifics.

Discussions of the function of cowbird head-down preening solicitation initially centered on heterospecific functions that may reduce the aggressiveness of cowbird host species (Selander and La Rue 1961). However, Rothstein (1977, 1980) showed that the head-down display also occurs in an intraspecific context, usually directed toward a behaviorally subordinate individual; although he found

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FIG. 1. Male Bronzed Cowbird (*Molothrus aeneus*, left) giving a head-down (preening invitation) display to female Great-tailed Grackle (*Quiscalus mexicanus*, right), 17 December 2003, Guamuchil, Sinaloa, Mexico.

that the displays were motivated by aggression, Rothstein (1980) reported that they were responded to as if they represented appeasement, thus constituting a form of behavioral mimicry. A display directed by a male Bronzed Cowbird toward a female grackle is similar to a display directed to a subordinate individual (S. I. Rothstein pers. comm.), even though the grackle is approximately 60% larger (Dunning 1992). Our midwinter observation of this display is not consistent with Selander and La Rue's (1961) argument that the display reduces interspecific aggressiveness from potential cowbird hosts. Scott and Grumstrup-Scott (1983) hypothesized that the head-down display is "an appeasing, agonistic behavior that reduces agonistic behaviors of the recipient toward the displaying cowbird." The displaying bird is generally dominant to the recipient, and preening may stimulate subsequent displaying by the preened cowbird. These authors cite possible social functions of this display relating to obtaining food, roost-

ing energetics, and/or maintaining flock order (Scott and Grumstrup-Scott 1983).

Although previous discussions about responses to head-down displays (e.g., Selander and La Rue 1961) relate to heteropreening, none explicitly mentioned foraging by the "preening" bird for ectoparasites on the displaying cowbird. We could not determine whether ectoparasites were actually obtained during our observation, but the female grackle's picking motions resembled foraging behavior rather than preening. Great-tailed Grackles exhibit a wide range of foraging behaviors (Johnson and Peer 2001), including taking ectoparasites from livestock (Skutch 1954). The Common Grackle (*Q. quiscula*) also has been noted picking leeches from the legs of map turtles (*Graptemys ouachitensis*; Vogt 1979).

As Rothstein (1977) pointed out, observations of preening solicitation behaviors in captive birds may not accurately reflect the context and functions of such behaviors in the

wild. Little is known of the importance of this behavior in wild cowbirds; as such, it is important to continue cataloguing the occurrence of such behavior and the identities of both the displaying bird and the recipient. Ours is among the few field observations of a head-down display performed by a Bronzed Cowbird, and it is the first report of such a display directed by a wild cowbird toward—and eliciting a response from—a Great-tailed Grackle.

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## Filial Cannibalism at a House Finch Nest

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**ABSTRACT.**—We report on a female House Finch (*Carpodacus mexicanus*) eating one of her own eggs from a clutch of six on the 3rd day of incubation. This observation is a confirmed case of filial cannibalism in the egg stage. The reason for this behavior is unknown, but we suggest and discuss three possibilities: (1) an idiosyncratic response to human disturbance, (2) removal of a damaged egg from the nest, and (3) facultative brood reduction in the egg stage. Received 12 January 2004, accepted 15 July 2005.

There are relatively few records in the literature of birds eating their own eggs, and we could find reports of this behavior for only seven species. The proximate causes for “filial cannibalism” in the egg stage (Stanback and Koenig 1992) can be classified as adaptive or nonadaptive. Adaptive behaviors include eating one’s own infertile (presumably) eggs that remain in the nest beyond normal incubation time (Walsh 1964, Berger 1981, Stiehl 1985, Banko et al. 2002), or eating eggs that have been damaged (Trail et al. 1981). In addition, female Acorn Woodpeckers (*Melanerpes formicivorus*) occasionally participate in eating their own eggs after those eggs have been removed from shared nests as an integral part of a unique, but apparently adaptive, communal breeding system (Mumme et al. 1983). In contrast, Chardine and Morris (1983) reported a presumably nonadaptive egg-eating behavior in Herring Gulls (*Larus argentatus*) after observing two males brooding at different nests eat their own eggs (at one nest, all eggs were eaten). This apparently abnormal behavior in the two males was at-

tributed, respectively, to a possible displacement response caused by a female gull returning late to her nest to brood, and to a possible idiosyncratic reaction to human disturbance.

Here, we report on a female House Finch (*Carpodacus mexicanus*) that ate a single egg from her clutch of six on the 3rd day of incubation. Timing of egg laying indicated that the egg was not laid by another House Finch (intraspecific brood parasitism is not known for the species; Hill 1993). We have no evidence that the eaten egg had been damaged, and it did not appear deformed, discolored, or undersized. We describe circumstances associated with the egg-eating event, and discuss possible causes for the behavior.

### METHODS

Observations were made on the campus of Auburn University, Auburn, Alabama, where wooden nest platforms (12 × 13 × 8 cm) were maintained under walkways and eaves of buildings. These platforms were open at the top and on one side and were designed to accept the bottom portion of 1.9-l plastic milk or juice containers (held in place by metal clips), which served as nest boxes. House Finches readily accepted the platform design, and typically built >60 nests each year at the study site. At various stages of the breeding cycle, video cameras were placed near some of the nests, usually ≤2 m away. These cameras provided good-quality video sequences, viewable with a freeze-frame feature. The video camera recording the event reported here was placed ~1.5 m from the nest at an acute angle from vertical, thus providing an excellent view. The House Finch pair at this nest was banded with a distinct combination of color bands that were readily identifiable in the videotape.

Each day, we examined those nests in which egg laying was occurring by using a mirror on an extended pole. We marked eggs at the large end with a nontoxic marker to

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indicate laying order. While examining nests for newly laid eggs, we were able to closely examine the upper sides of all eggs; eggs removed from nests during marking were thoroughly inspected by hand. After clutches were complete, we inspected nests every 2 days using a mirror on a pole.

### OBSERVATIONS

The video camera at the House Finch nest site recorded the following events at 08:35 EST on 19 April 1997, the approximate start of the 3rd day of incubation ( $n = 6$  eggs). The resident male landed at the nest and briefly fed the resident female. Both birds then flew off for about 30 sec. The resident female, positively identified in the video by her color bands, then returned to the nest and appeared to inspect the nest contents. She then bit into one of the eggs and began to eat it. She continued eating for approximately 3 min and then perched on the edge of the nest for about 1 min with the eggshell in her beak. She then flew off, carrying the eggshell with her.

Subsequent examination showed that the egg had been the third one laid. It was 6 days old when eaten, had been incubated for 2 days, and was normal in size, shape, and color. The six eggs in the clutch were laid at 1-day intervals over 5 days. After the egg-eating event, no additional eggs were lost from the nest, and the pair hatched and fledged the remaining five young.

Six-egg clutches made up only 5.5% (12/217) of all clutches observed at the study site, whereas five-egg clutches composed 55% (119/217), four-egg clutches 29% (63/217), and three-egg clutches 5% (11/217). The male of the pair was 2 years old; the female's age was unknown. Our records do not indicate whether we had hand-inspected the eaten egg after the day it was marked, but all eggs had been viewed from above. We observed no defects in any of the six eggs from the time the final egg was laid through the time of camera installation early on 19 April; videotape recordings made before the egg-eating event also revealed no defects.

### DISCUSSION

The egg-eating event we report represents a case of filial cannibalism in the egg stage (Stanback and Koenig 1992), a behavior for

which there are few published records for birds. We propose three possible explanations for this behavior. First, it may have been an idiosyncratic, and presumably nonadaptive, response by the female House Finch, perhaps to human disturbance (Chardine and Morris 1983). The most likely human disturbance would have been the placement of the video camera on the morning the egg was eaten. However, video cameras had been placed near 63 other House Finch nests during the study with no apparent abnormal responses (PMN unpubl. data). Also, two other nests from which single eggs disappeared did not have cameras placed near them.

Second, the female House Finch may have eaten one of her eggs because it had been damaged, perhaps punctured, during marking. There is at least one published report of a female bird eating one of her own eggs after it was damaged (Trail et al. 1981). However, we detected no damage to the egg, and even if the female House Finch had detected damage unnoticed by us, it is uncertain that she would have removed and eaten the egg.

Third, the female House Finch may have eaten one of her own eggs to reduce the size of her clutch. Six-egg clutches in House Finches are rare (5.5% of total), whereas four- and five-egg clutches are common. Clutch sizes larger than normal could be a trigger for female House Finches to remove eggs. In fact, the proportion of single eggs disappearing from six-egg clutches (2/12; including the six-egg clutch discussed above) differed from the proportion disappearing from smaller clutches (1/205; from a five-egg clutch; Fisher exact test,  $P = 0.008$ ; PMN unpubl. data).

When brood reduction occurs in bird nests, it usually happens during the nestling stage, and sometimes involves filial cannibalism (e.g., Ricklefs 1965, Ohmart 1973, O'Conner 1978, Mock and Parker 1986). In some *Eudyptes* penguin species, brood reduction regularly occurs in the egg stage, but it does not involve filial cannibalism (St. Clair et al. 1995). In some non-avian taxa, however, brood reduction occurs in the egg stage and involves filial cannibalism (Mock and Parker 1997).

Our observation of a House Finch eating her own egg is a confirmed case of filial cannibalism in the egg stage. However, we were unable to determine whether it was (1) an idiosyn-

cratic, nonadaptive response, presumably due to human disturbance; (2) an adaptive response to eliminate a damaged egg; or (3) an adaptive response to reduce clutch size. Studies of House Finch responses to disturbances near active nests, deliberate egg puncturing, and artificial increases in clutch size would shed light on the causes of filial cannibalism in House Finches.

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## An Observation of Foliage-bathing by an Orange-breasted Falcon (*Falco deiroleucus*) in Tikal, Guatemala

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**ABSTRACT.**—I observed a pair of Orange-breasted Falcons (*Falco deiroleucus*) in Tikal, Guatemala, on 30 December 2003 and 1 January 2004. I observed the birds flying through wet foliage as a means of bathing, which has not been described previously for this species. During a morning with light rain, an adult falcon took off from a perch, flew low over the forest canopy, and appeared to crash intentionally into the wet, upper foliage of emergent trees before returning to its perch. I observed three repetitions of this behavior. Received 16 November 2004, accepted 13 July 2005.

The Orange-breasted Falcon (*Falco deiroleucus*) is a little known and rare Neotropical falcon (Collar et al. 1994, Baker 1998, Baker et al. 2000, Thorstrom et al. 2002). Using a 10 × 42 binocular, I observed a pair of Orange-breasted Falcons in Tikal, Petén, Guatemala (17° 14' N, 89° 37' W) on 30 December 2003 and on 1 January 2004. This species is often confused in the field with the Bat Falcon (*Falco ruficularis*; Jenny and Cade 1986, Howell and Whittaker 1995; D. F. Whitacre in litt.). However, the bird's bulky shape, which resembles that of a Peregrine Falcon (*F. per-*

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*egrinus*), and its extensively orange chest allowed me to make a positive identification (photographs of one of the Orange-breasted Falcons described herein are available online at <http://www.cayaya-birding.com/pubs.htm>). Tikal is an ancient Mayan city, characterized today by pyramids (up to 65 m tall) surrounded by semi-deciduous lowland broadleaf forest. Ascending some of the pyramids permits a view over the forest canopy, which is ~30 m tall. Dispersed emergent trees rise 15 m above the canopy. Nesting of the Orange-breasted Falcon in the ancient Mayan buildings of Tikal has been reported by Smithe (1966), Boyce (1980), and Baker et al. (2000). The initiation of courtship in northern Petén and Belize occurs in January and February (Baker 1998).

On 30 December 2003, at 09:00 CST, I observed courtship behavior of a pair of Orange-breasted Falcons from ~30 m away in the "Lost World" complex of Tikal. When first observed, one falcon—perched on a branch stub in the upper part of a 40-m-tall tree—left a piece of an unidentified bird prey item before flying off. The second bird then landed on the prey and began feeding on it. I assumed the second bird was the female, because prey transfers are reported to occur from male to female (Baker 1998). I never saw both birds close enough to each other to judge size differences (females are larger than males; Howell and Whittaker 1995, Baker 1998). Because both falcons were vocalizing from tree perches ~40 m apart, the size and color pattern of both birds appeared to be similar. Prey transfers were also observed on several days in April 2004 at the entrance of the assumed nesting cavity on Temple IV, 500 m northwest of the Lost World complex (M. Córdova pers. comm.)

On 1 January 2004, at approximately 08:00, I observed foliage-bathing behavior from where I was standing at the upper landing of Temple IV in Tikal. During a light rain, one Orange-breasted Falcon perched on top of a snag, 300 m away from the temple, and a second falcon perched on the top of the temple, where I detected it by its calls; I was unable to distinguish the gender of either bird. The falcon that was perched on the snag flew off low over the canopy. It gained elevation before reaching an emergent tree and crashing

into the wet upper foliage. What appeared at first to be accidental turned out to be an intentional behavior that I interpreted as bathing. The falcon continued flying and again crashed into the upper foliage of another emergent tree ~200 m away before returning to its original perch, where it shook and repeatedly ruffled its feathers. I did not observe any active preening. After several minutes, the same falcon flew off again and crashed twice more into the same group of trees. I observed this behavior three times over a period of 10 min. An obvious splashing of water drops was visible during each crash. Sometimes the falcon stretched out its legs shortly before reaching the emergent tree and grasped a twig, letting itself fall into the wet foliage before continuing the straight-line flight into the next tree.

The possibility that the observed behavior was an unusual way of capturing prey almost certainly can be excluded, because I did not see the falcon holding anything in its feet when it left the tree, nor was it eating during the flight or on the perch after landing again. Given that the observation was made at the beginning of the breeding season, the spectacular crashing was possibly part of courtship behavior. Jenny and Cade (1986) and Baker (1998) found that females spend most of their time near the nest area during courtship and incubation, and males deliver food to them. The observed bathing might have been a male's display flight—an advertisement of its fitness for obtaining prey during the nesting season. Baker (1998) described display flights as strong flapping flights in front of cliffs—with rare rolling to either side—and diving flights obviously not directed at prey.

There appear to be no published descriptions of bathing behavior in Orange-breasted Falcons, although a similar bathing behavior has been described by Meinecke (1993) for a Eurasian Hobby (*Falco subbuteo*), which was flying in circles around two solitary broadleaf trees during a light rain. That falcon repeatedly clung to the outer twigs, letting itself fall—with wings spread—into the wet foliage beneath. Grünhagen (1983) observed two juvenile Eurasian Hobbys falling into wet foliage, although it appeared that the birds fell because the small twigs on which they had perched could not support them. Barreto

(1968) reported a captive Bat Falcon bathing by rubbing against wet foliage.

Most reports of bathing falcons are based on observations of ground bathing in shallow water (Taverner 1919, Fischer 1977, Heller 1985, Christen 1986, Holthuijzen et al. 1987, Glutz von Blotzheim et al. 1989, Sodhi et al. 1993, Clum and Cade 1994, del Hoyo et al. 1994, Keddy-Hector 2000, Smallwood and Bird 2002, White et al. 2002). The few reports of other bathing strategies during flight include a Peregrine Falcon flying through mist from waterfalls (White et al. 2002) and a Eurasian Hobby and a Peregrine Falcon flying through a light rain (Fiuczynski 1988 and Fischer 1977, respectively). Ristow et al. (1980) reported juvenile Eleonora's Falcons (*F. eleonora*) bathing in the rain while standing in their nest, and Sodhi et al. (1993) reported a Merlin (*F. columbarius*) bathing in the rain with its wings and tail extended.

Falcons (*Falco* spp.) are generally considered birds of open habitats (del Hoyo et al. 1994). Although the Orange-breasted Falcon is restricted to tropical forest (Cade 1982), it mainly uses the open space over the canopy and that along nearby rock cliffs and rivers (Jenny and Cade 1986, Whittaker 1996, Baker et al. 2000). Small pools of water occur near Tikal, but there are no larger water bodies offering open space. To my knowledge, the Orange-breasted Falcon has not been reported to enter the forest below the canopy, and it seems unlikely that the birds would bathe at small pools within the forest, entering a habitat unfamiliar to them. Therefore, it appears that bathing in rain and foliage, or in puddles on top of the Mayan ruins, are the only alternatives for Orange-breasted Falcons in Tikal.

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## Bare-necked Umbrellabird (*Cephalopterus glabricollis*) Foraging at an Unusually Large Assemblage of Army Ant-following Birds

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**ABSTRACT.**—I observed a juvenile male Bare-necked Umbrellabird (*Cephalopterus glabricollis*) forage on arthropods flushed by a large swarm of the army ant *Eciton burchellii* in the Caribbean foothills of Costa Rica. Apparently, this is the first report of this species attending an army ant swarm. At least 60 birds of eight different species were foraging at that swarm, the largest assemblage of army ant-following birds reported in the Neotropics. *Received 13 October 2004, accepted 1 July 2005.*

The Bare-necked Umbrellabird (*Cephalopterus glabricollis*; Cotingidae) is an elevational migrant endemic to forests of the Caribbean slope of Costa Rica and western Panama (Snow 1982, Ridgely and Gwynne 1989, Stiles and Skutch 1989). Entire populations of this species spend the breeding season (February–July) in the highlands and then migrate to the lowlands, where they remain for at least 6 months (Chaves-Campos et al. 2003). The species feeds on fruit, large arthropods, and small vertebrates (Snow 1982, Ridgely and Gwynne 1989, Stiles and Skutch 1989; JC-C

pers. obs.). The possibility of extinction is high because of recent destruction and/or fragmentation of lowland habitats (Benstead et al. 2004), which may severely reduce the availability of food sources for populations during the nonbreeding season; however, little is known about the diet of this species when it inhabits the lowlands (Chaves-Campos et al. 2003). Documenting food resources could promote conservation strategies designed to protect this species.

On 13 January 1999, from 08:00 to 09:15 CST, in the foothills of the Tilarán Mountains, Costa Rica, I watched a juvenile male Bare-necked Umbrellabird forage over a swarm of army ants (*Eciton burchellii*; see Bolton 1995). The site was located at 400 m above sea level, the lowest elevation where forest still remains on the Caribbean slope of the Tilarán mountain range (see Chaves-Campos et al. 2003 for a description of the site). The bird perched on tree branches 3–4 m above ground, catching large arthropods flushed by a column of ants that climbed the tree trunk above the main swarm. This swarm was particularly large (about 12 m wide) and the assemblage of ant-following birds was noteworthy. Although it was difficult to estimate the numbers of foraging birds due to

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their constant movement, I estimated at least 20 Ocellated Antbirds (*Phaenostictus mcleannani*), 10 Bicolored Antbirds (*Gymnophrys leucaspis*), 10 Spotted Antbirds (*Hylophylax naevioides*), and 10 Plain-brown Woodcreepers (*Dendrocincla fuliginosa*) attending the swarm at the same time. In addition, I recorded a few Northern Barred-Woodcreepers (*Dendrocolaptes sanctithomae*), Rufous Motmots (*Baryphthengus martii*), and White-fronted Nunbirds (*Monasa morphoeus*).

This is the largest assemblage of army ant-following birds reported for the Neotropical area, comparable only with assemblages of African birds at large swarms of *Dorylus* spp. driver ants (E. O. Willis pers. comm.). Large assemblages of army ant-following birds in the Neotropics are usually composed of no more than 20–30 individuals (Oniki 1971, Gochfeld and Tudor 1978, Dobbs and Martin 1998, Wrege et al. 2005; JC-C pers. obs.). The simultaneous presence of 10 or more obligate ant-following birds of the same species at the same swarm also constitutes an extraordinary event (see Swartz 2001, Chaves-Campos 2003, Willson 2004). The observation of a Bare-necked Umbrellabird is unusual as well.

To the best of my knowledge, this is the first report of a Bare-necked Umbrellabird foraging at a swarm of army ants. Members of the family Cotingidae rarely follow army ants, perhaps because they generally do not inhabit, or forage in, the forest understory (Willis 1983, Willis and Oniki 1992). However, Bare-necked Umbrellabirds sometimes eat fruits close to the forest floor (1–3 m above ground; JC-C pers. obs.), suggesting that they might be more inclined to take prey flushed by swarms of army ants than other cotingids (e.g., more so than cock-of-the-rock *Rupicola* spp., which occasionally forage at army ant swarms; E. O. Willis pers. comm.). Thus, the presence of the Bare-necked Umbrellabird at this swarm suggests that it might be an occasional ant follower.

The absence of previous reports regarding Bare-necked Umbrellabirds in association with swarms of army ants could be due to a number of factors: low abundance and small geographic range for this bird species, characteristic elevational migratory behavior, and/

or the lack of research conducted on umbrellabirds during seasons when they inhabit the lowlands. I sampled umbrellabird abundance seven times during 1998–1999 (see Chaves-Campos et al. 2003), and this was the only occasion on which I saw army ants.

I speculate that Bare-necked Umbrellabirds may follow swarms of army ants primarily during the nonbreeding season, when the umbrellabirds are in the lowlands. Army ants seem to flush more insects in the lowlands than in the highlands (JC-C pers. obs.), probably because the abundance and size of their colonies decreases with increasing elevation (Hilty 1974, Gochfeld and Tudor 1978). In addition, they seem to flush more insects during the rainy season (Willis and Oniki 1992)—particularly on trees (Willson 2004)—when Bare-necked Umbrellabirds migrate to the lowlands (Chaves-Campos et al. 2003).

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# Ornithological Literature

Edited by Mary Gustafson

**THE REMARKABLE LIFE OF WILLIAM BEEBE: EXPLORER AND NATURALIST.** By Carol Grant Gould. Island Press, Washington, D.C. 2004: 447 pp., numerous photos, index. ISBN: 1559638583. \$30 (cloth).—In this biography, Carol Grant Gould chronicles the long, productive life of William (Will) Beebe—a man with a driven personality, one who suffered from bouts of depression, but who was usually charming and charismatic—a complicated but insightful person. Gould had at her disposal Beebe's journals that he wrote from boyhood to old age, and the personal papers of Jocelyn Crane, Beebe's colleague and companion during Beebe's later years. These documents, not available to earlier biographers, allowed Gould to present new insights into the life of William Beebe and into the changes in natural history studies and focus that occurred as the Victorian era came to a close and natural history matured during the first half of the twentieth century. Gould describes the scientific aspects of Beebe's work effectively and handles the difficult personal aspects of his life—such as his estrangement from his first wife—with sensitivity, thus projecting a very credible story of a remarkable ornithologist and natural historian.

The book is divided into four parts: Naturalist, Ornithologist, Marine Biologist, and Tropical Ecologist. Part I, Naturalist, traces Beebe's life from his birth in 1877 through his formative years as he developed an obsession for all things natural; he collected everything from seashells to stuffed birds while “bugging” and “fossiling” with his friends. He attended Columbia University, where he was mentored by Henry Fairfield Osborn, prepared bird skins, and was sponsored for membership in the American Ornithologists' Union by Frank Chapman. He eventually left Columbia to take a job tending birds at the new Bronx Zoo.

Part II, Ornithologist, covers Beebe's early ornithological exploits. In 1904 he married, and his honeymoon consisted of a rugged expedition to Mexico that resulted in the publi-

cation of his first book, *Two Bird Lovers in Mexico* (1905, Houghton Mifflin, Boston, Massachusetts). Beebe became a prolific writer, producing 24 books and hundreds of scientific papers and popular articles. In 1906, he published *The Bird: Its Form and Function* (Henry Holt, Garden City, New York). Most of his books had at least some focus on birds.

Under Osborn's mentorship, Beebe became a favorite of the New York Zoological Society, which directed the Bronx Zoo, and through lectures and articles, he became well known to the high society that funded major projects, including scientific expeditions. Beebe also had a strong relationship with the American Museum of Natural History, and became a confidant of Theodore Roosevelt. All this led to funding for a series of expeditions to northern South America, and an expedition around the world to study pheasants for more than a year. That trip culminated in his four volumes: *A Monograph of the Pheasants* (1918–1922, H. F. Witherby, London, United Kingdom). Other tropical adventures involved establishing a research station in what was then British Guiana, where he collected animals for the Bronx Zoo and conducted research on a broad spectrum of animals and plants. Although his first love was always birds, he was the consummate natural historian. World War I disrupted his adventure in British Guiana, as he trained pilots for the war and eventually flew over the battle zones of France. After the war, he returned to British Guiana to set up another tropical research station under the auspices of the New York Zoological Society.

Part III, Marine Biologist, deals with Beebe's adventures in marine biology, especially his descent in the bathysphere to more than a half mile below the surface of the Atlantic Ocean near Bermuda. This earned Beebe international notoriety. With Part IV, Tropical Ecologist, we return to an ornithological and more general focus on natural history. During and after World War II, Beebe established several research stations, culminating with Ran-

cho Grande, a cliffside ruin in the Andes west of Caracas. Three winters at Rancho Grande led to one of Beebe's best books, *High Jungle* (1949, Duell, Sloan and Pearce, New York). Jocelyn Crane did most of the searching for a new research station and found one in Trinidad that Beebe bought and donated to the New York Zoological Society. Simla, as Beebe named the estate, became his major place of residence for the remainder of his life. Beebe invited a succession of researchers to Simla, including Konrad Lorenz, Barbara and David Snow, Lincoln Brower, and Donald Griffin. In 1962, with Jocelyn by his side, Beebe succumbed to pneumonia.

In the Epilogue, Gould comments on Beebe's contributions to science: "The effects William Beebe had on science . . . are enormous and lasting. He made an effective transition between Victorian natural historian, content to collect and classify the natural world, and the modern experimental biologist. . . . His early conviction of the truth of Darwin's theory of natural selection shaped his enquiry into the lives of pheasants, the embryology of fish, and the phenomenon of mimicry, and led him to make pioneering studies of selection on the Galapagos." In addition, through his popular books and papers, Beebe influenced several generations to develop an interest in natural history. As a boy, I read most of Beebe's books and was strongly influenced by them. In 1961, I was privileged to spend an afternoon with William Beebe and Jocelyn Crane at Simla and listen to him recount many of the stories I had read in his books a decade before.

This book is well written, thorough, and a great read. The *Selected Bibliography* just scratches the surface of Beebe's writings, but another section, *Books and Articles by Other Authors*, includes Robert Welker's previous biography *Natural Man: The Life of William Beebe* (1975, Indiana University Press, Bloomington) and Tim Berra's *William Beebe: An Annotated Bibliography* (1977, Archon Books, Hamden, Connecticut) for those who wish to delve deeper into the life of this fascinating man. For those with a biographical bent, this is a must read.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

HANDBOOK OF WESTERN AUSTRALIAN BIRDS, VOLUME II: PASSERINES (BLUE-WINGED PITTA TO GOLDFINCH). By R. E. Johnstone and G. M. Storr. Western Australian Museum, Perth. 2004: 529 pp., 28 color egg plates, 34 color bird plates, numerous line drawings, 3 appendices. ISBN: 1920843116. A\$130 (cloth).—Western Australia, one of seven Australian states, occupies about a third of the Australian continent, and is characterized by an entirely different climate and vegetation in its northern and southern sections. Its climatic zones range from humid to desert. Hence, the avifauna varies from resident to migratory to nomadic, and occupies three zoogeographic divisions: northern tropical, southwestern temperate, and central arid zones. Detailed descriptions of climate, physical features, vegetation, and a general discussion of Western Australian avifauna are not included in this volume because they were covered thoroughly in volume I (1998); it does, however, include maps of the three zones and a map depicting biogeographical regions and botanical provinces. This volume summarizes what is known about the 255 species and subspecies of passerine birds that occur there.

The book is large (23 × 32 cm) and lavishly illustrated. Species accounts occupy the bulk of the book (364 pp.). Each of the 32 families is described briefly, usually with two or three sentences. The species accounts are thorough and comprehensive, drawing on thousands of records and measurements of all specimens in the Western Australian Museum plus many other collections. Species accounts typically include names in past and current usage; a description of plumage; measurements of weight and total length; distribution, habitat, and status; food habits and diet; breeding biology; vocalizations; geographic variation and taxonomy; and relationships with other species. Whether a bird is resident, migratory, or nomadic is discussed under *Status*, and foraging behavior is covered under *Food*. Interesting behaviors, such as communal roosting in woodswallows (*Artamus* spp.), are presented in a section of *Remarks*. Range maps show the distributions of subspecies, hybrid zones, and wintering and breeding areas, with arrows indicating migration or nomadic movements. Excellent line drawings by Martin Thompson

and Trish Wright of nests for nearly all breeding species accompany the species accounts. The color plates by Martin Thompson are outstanding and depict plumage differences among sexes, age groups, subspecies, and geographical differences, with up to 10 images per species. The egg plates consist of color photographs of egg clutches, presented actual size, and often including four or five clutches per species.

Three appendices follow the species accounts. Appendix A is an annotated checklist of Christmas Island birds. Christmas Island is 1,400 km from Western Australia but is administered by the Commonwealth of Australia. The island has 23 breeding species and 104 visitors and vagrants. The 37 pages of Appendix A consist mostly of species accounts and four colored plates painted by John Darnell. Appendix B is an annotated checklist of Cocos-Keeling Islands birds, consisting of 18 pages of species accounts. Appendix C contains species accounts of birds reported for Western Australia since 1998, when volume I of the handbook was published. A glossary, a gazetteer of Western Australian locations, a bibliography of nearly 500 titles, and an index conclude the volume.

I find little to criticize in this book, but the lack of in-text citations (a sacrifice to readability, I presume) makes it difficult to match references in the bibliography with individual species. I also would like to have seen the bibliography contain a more complete set of references to bird behavior and community structure. Aside from these details, this is a handsomely produced, well-written, and exhaustively researched book. It should be part of every academic library and the library of anyone who has a serious interest in Australian birds.—WILLIAM E. DAVIS, JR., Boston University, Boston, Massachusetts; e-mail: wedavis@bu.edu

**THE BIRDS OF AZERBAIJAN.** By Michael Patrikeev. Edited by Geoffrey H. Harper. Pensoft Series Faunistica No. 38, Sofia, Bulgaria. 2004: 380 pp., 241 distribution maps, 6 graphs, 80 photographs (3 black/white, 77 colored). ISBN: 954642207X. \$85.16 (cloth). This large-format (21.5 × 28.5

cm), remarkably informative book is the first monographic description of Azerbaijan birds. The author claims that it is not a comprehensive handbook, but it is scholarly and primarily a broad historical, biogeographical, and ecological treatment. It is a welcome and needed addition to the ornithology of this fascinating, and hitherto little known, area of the southern Palearctic. Azerbaijan is a relatively small country of 86,000 km<sup>2</sup> in Eastern Transcaucasia, bordering the western shore of the Caspian Sea. The book contains no species-specific measurements or identification descriptions, but this information is readily available from numerous European field guides. What it does contain is valuable fundamental knowledge, and guidance and encouragement for future bird conservation and management. The author's hope seems to be that birds will do for Azerbaijan what they have done for other countries: contribute to protecting not only the avifauna, but also the resources needed to rehabilitate and sustain healthy ecosystems.

The book begins with a geographic description of the country and its associated avian habitats, a historical review of Azerbaijan ornithology, an overview of the country's avifauna from the mid-1800s to the late 1900s, and a description of seven avifaunal geographic regions and subregions. It then provides a revealing assessment of bird conservation in this developing nation, one with a diverse birdlife and extraordinary human turmoil. The species accounts follow and include most of the text (pp. 35–284). The accounts include summaries of distribution (usually including a map), population size, movements, breeding ecology, diet, causes of mortality, behavior, and status (abundance, endangered or declining, seasonal occurrence, and taxonomy). The photographic plates, presented without obvious organization, depict selected habitats, nests, and flocks or individual birds. The photo of the Calandra Lark (*Melanocorypha calandra*) nest containing young is certainly one of the most striking examples of concealment.

Eight appendices follow the plates and include (1) a systematic species list containing information on abundance and seasonal occurrence; (2) a description of 51 Important Bird Areas (IBAs) that, for select IBAs, in-

clude tables detailing numbers of birds per species over time; (3) a list of colonial waterbirds at selected wetlands—primarily for three prominent sites (Kalinovsky Liman-Lopatinsky Marsh, Lake Aggel, Lake Mahmud-chala)—for which numbers of birds by species are tabulated and for which graphs of changes in species composition over time are presented; (4) a description of waterfowl hunting; (5–6) an assessment of the consequences of cold winters and oil pollution for birds; (7) a glossary of Azeri and Russian words used in the text; and (8) a comparison of spelling differences for geographic names published in the text and used in standard atlases. Following the appendices is an extensive reference section containing many non-English citations, the titles of which are translated into English. The work concludes with indices of species' English and scientific names.

We learn from Patrikeev that in 1773, S. G. Gmelin made the earliest documented ornithological observations in Azerbaijan. In the early 1800s, E. Menetries was the first naturalist to collect specimens, describing three new species: Marbled Teal (*Marmaronetta angustirostris*), Bimaculated Lark (*Melanocorypha bimaculata*), and Menetries's Warbler (*Sylvia mystacea*). In the mid-1800s, the Italian F. deFilippi collected specimens in what is now Azerbaijan, and the Caucasian Museum was established in what is now Tbilisi, Georgia; its first curator, Gustav Radde (a German in Russian service), and his successor, K. A. Satunin, studied the avifauna throughout the Caucasus region, including Azerbaijan, in the early 1900s. From the 1930s to the 1960s, K. Gambarov of the Institute of Zoology, Academy of Science of Azerbaijan, conducted bird studies, including the first to address the effects of oil pollution. From 1950 to 1970, several authors focused primarily on the study of economically important species. During the 1960s to 1980s, Gara Mustafaev of Azerbaijan University (Baku) was the leading avian researcher investigating the nation's avifauna. Patrikeev's principal fieldwork occurred from 1988 to 1991, and most of what is in *The Birds of Azerbaijan* are his previously unpublished results of that period. Although bird study has a long history in Azerbaijan, even increasing in modern times, most of the coun-

try awaits detailed ornithological attention, which promises intriguing discoveries.

Currently, 372 bird species (17 orders and 58 families) have been recorded in Azerbaijan; they comprise 107 permanent residents, 139 summer residents, 95 migrants and winter residents, 28 accidentals, and 3 extirpated species. Another eight species are unconfirmed. Historic and current threats to the country's birds include hunting, habitat loss or degradation, pollution, and depredation. Sacred Ibis (*Threskiornis aethiopicus*), Lanner Falcon (*Falco biarmicus*), and Pin-tailed Sandgrouse (*Pterocles alchata*) are thought to be extirpated. There also are 9 endangered, 11 threatened, 39 rare, and 10 vulnerable species; in addition, 10 have restricted ranges, there is insufficient information for 14, and 12 no longer breed and 2 no longer overwinter in the country. Among the common species, 12 are declining, 8 are increasing, and 7 are undergoing range extensions. From the 1950s to present, four new species have nested and four others were recorded in the country for the first time. Patrikeev informs us that species with positive population trends are wide-ranging and tolerant of human activities, whereas species whose populations are declining or are already greatly diminished have specific habitat requirements or are intolerant of habitat degradation.

About 5% of Azerbaijan's land is designated as nature reserves (185,000 ha) and game preserves (250,000 ha) that purport to protect birds and other life within their borders. Patrikeev then disappointingly describes how laws are abused or ignored throughout the country, primarily because of paralyzing economic and political instability. Poachers openly take birds and other animals from protected areas; in 1989–1990, 600–700 poachers at one reserve hunted waterfowl without limit, and hunting overall continues unabated or unregulated. The extravagant toll that oil pollution is taking on birds and the entire Caspian Sea ecosystem is gravely alarming. Moreover, we learn that the Azerbaijan government policy toward natural resource conservation remains unknown, and, by inference, it appears that conservation education is meager to nonexistent in schools or for the general public. Still, Patrikeev hopes that government stability and a core of committed citizens will de-

velop, eventually resulting in effective protection for all the nation's natural resources.

There are a few typos, some notable omissions (such as the incomplete numbering of photographs), and no pagination on the plates (pp. 289–318; page numbers for the plates are in the indices). Notwithstanding these slips, the work is relatively error free. Despite the seemingly random order of the plates, they are attractive and instructive. The distribution maps can be difficult to interpret because the shades designating different occurrence areas (main wintering grounds, other wintering grounds, historical wintering areas) are similar enough to be confusing when viewing one map after another, or when viewing several maps over several different pages where only some of the shading categories are used. Although breeding locations are distinctly noted, breeding ranges are unclear, as there are no labels denoting breeding ranges in the map legends.

Aside from these shortcomings, this book is an outstanding achievement and a valuable contribution to bird study in a part of the world that is, to date, only modestly known to most ornithologists and other bird students, especially in the West. In my view, this work is a must for institutional libraries everywhere, but especially for teaching and research institutions, for conservation professionals interested in birds, and for those interested in conserving the natural world in developing countries. The plates give one a good sense of the landscape and depict some of Azerbaijan's most attractive birds. The book will appeal to all readers, especially those who will visit Azerbaijan to birdwatch when it is safe to do so.—DANIEL KLEM, JR., Muhlenberg College, Allentown, Pennsylvania; e-mail: klem@muhlenberg.edu

**SHOREBIRDS OF NORTH AMERICA: THE PHOTOGRAPHIC GUIDE.** By Dennis R. Paulson. Princeton University Press, Princeton, New Jersey. 2005: 384 pp., 534 color photographs. ISBN: 0691102740, \$65 (cloth). ISBN: 0691121079, \$29.95 (paper).—As stated in the preface of this new guide, shorebirds are among our most engaging birds. Their ecology and behavior are the sub-

jects of numerous ornithological studies, their identification can challenge the skills of the most serious birdwatchers, and people with a casual interest in birds are captivated by the antics of Sanderlings (*Calidris alba*) chasing waves along a beach. While some books provide a worldwide perspective on shorebird identification, this book is the first guide devoted solely to identifying every species occurring in North America. Its coverage is truly continental, extending from Alaska to Panama and including the West Indies.

This book is strictly an identification guide. The *Introduction* contains information on topics such as anatomy, molt, sexual variation, behavior, and vocalizations, but these topics are addressed within the context of how they pertain to the field identification of shorebirds. Most of the text is devoted to accounts for the 94 species that have been sighted in North America, beginning with Double-striped Thick-knee (*Burhinus bistriatus*) and ending with Oriental Pratincole (*Glareola maldivarum*).

To the author's credit, the same level of information is provided for every species, regardless of its status in North America. The 1–2 pages of text per account cover size, subspecies, plumages, in-flight characteristics, voice, behavior, habitat, and distribution. The amount of detail included in the plumage descriptions varies among species but tends toward statements emphasizing general distinguishing characteristics rather than feather-by-feather details. Each account is accompanied by a series of color photographs illustrating the various plumages and field marks. Most species are portrayed in 4–7 photos, with as many as 11 for a few species with complex plumage patterns or that pose considerable field-identification challenges. These photos are invariably of excellent quality and the color reproduction appears very good, at least to my eye. The captions discuss specific field marks evident in each photograph, frequently covering details not mentioned elsewhere in the account. The book ends with a 3-page list of references, which is by no means a complete compilation of the relevant shorebird identification literature.

My biggest complaint is the failure to summarize the key identification features for a species in one easily located section of each

account. The identification information is definitely provided, but the user may have to wade through the identification, plumage, and possibly subspecies sections and every photo caption to gather all of the pertinent details—no easy task when struggling with the identification of a difficult shorebird in the field. Other criticisms are relatively minor. No subspecies descriptions were provided for Greater Sand-Plover (*Charadrius leschenaultii*), a serious omission when needing to separate some races of this species from potentially similar races of the Lesser Sand-Plover (*C. mongolus*)—a problem most North American birders can only dream about. Similar flaws are rare.

The amount of information would likely overwhelm a true beginner who should probably use a field guide with fewer details. However, for novice to expert birders with a passion for shorebirds, this book will likely become their standard identification reference.—BRUCE PETERJOHN, USGS Patuxent Wildlife Research Center, Laurel, Maryland; e-mail: bpeterjohn@usgs.gov

**PIPITS AND WAGTAILS.** By Per Alström and Krister Mild, illustrated by Per Alström and Bill Zetterström. Princeton University Press, Princeton, New Jersey. 2003; 496 pp., 30 color plates, and 240 color photographs in 40 plates. ISBN: 0691088349. \$67.50 (cloth).—This book covers two closely related, but rather disparate, groups of birds: the wagtails—spectacular and charismatic, usually brightly colored in blacks and yellows or strikingly patterned in black and white; and the pipits—no less engaging, but whose plumage is invariably streaked or spotted brown. Wagtails rarely present identification problems; by contrast, more ink and bile has been expended, and more reputations made or lost, on pipit identification (they are famous vagrants) than on almost any other group of birds. To quote some amusing doggerel first published many years ago in the *Ringers' Bulletin* (the house magazine of British bird banding), “It’s a pity that the pipits have / No diagnostic features, / Specifically they are the least / Distinctive of God’s creatures.”

The book begins with a useful introduction, including such “nuts and bolts” items as spe-

cies concepts (biological versus phylogenetic), the terminology applied to sonograms and topography, a glossary of technical terms, comprehensive treatments of molt and ageing, and nomenclature. Some of these sections, all clearly written and of general application, should be compulsory reading for any first-year student of ornithology, with or without any specific interest in this family of birds.

Thirty color plates follow the introduction, with 7–17 illustrations on each plate. Given that fewer than 30 species are covered, the plates are enormously detailed and comprehensive. Special care has been taken to group together species easily confused during identification, with many figures positioned to emphasize plumage features of the back and face that would be missed in the conventional broadside postures of most field guides. The quality of artwork is consistently high and the two artists work together seamlessly.

The bulk of the book (331 pages) is devoted to individual species accounts. These vary in length from 3 pages for the little-known Berthelot’s Pipit (*Anthus berthelotii*)—endemic to the Canaries and Madeira—to 49 pages for the White Wagtail (*Motacilla alba*) complex. Species accounts include sections on distribution; identification (which, given the racial complexity of some species, is itself a study); detailed plumage descriptions for all ages and both sexes of the nominate race, followed by highly detailed treatments of geographic variation; systematics, molt, ageing, and sexing; and behavior, distribution, and habitat. There are large sections in each species account on voice, which are major studies in their own right; for the White Wagtail complex there are 43 individual sonograms, and for the Yellow Wagtail, 34. Many readers will find these a little excessive, but for any serious student they will be the definitive study. What is not given in the species accounts is any treatment of nests and eggs, which would indeed have been of interest to the more general reader, albeit at the expense of making the book larger and more expensive. A distribution map accompanies each species; in contrast to so many other works, the maps have been prepared with extreme care and much attention to detail (e.g., the two superbly detailed maps for the Long-billed Pipit, *Anthus similis*), with political boundaries and major rivers marked,

making interpretation easy. For some species, maps of wintering ranges—separated according to subspecies—are also provided. My main criticism of the section on *Distribution* (which includes information about migration) is that for several species, such as White or Yellow wagtails, it would have been greatly enhanced by reference to the large database of recoveries that exists for birds banded not only in Europe but also, to a lesser extent, in Israel and East Africa.

One pleasing feature of the book is how references have been treated; in many other books of this type, references are clustered together at the end of a species account, making it impossible to link individual references to a specific statement in the text. That is not the case in this book; although an *Additional Literature* section is given at the end of each species account, individual references are linked to specific statements—a practice that all such works should follow. Given that the bibliography runs to about 500 individual citations, how they are presented is a major issue.

Toward the end of the book are 40 pages of photographs, 6 per page, accompanied by

explanatory text; additionally, there are more sets of photographs embedded in the text, illustrating such things as the wing patterns on the flight feathers of wagtails. These photographs are especially useful in combination with the painted illustrations, which depict birds in ideal postures. In the real world, birds are rarely that cooperative. The photographs, with all the usual variations in lighting, background, and activity, give a more realistic idea of the problems with pipit identification, lest the reader get an impression that it is too easy! In fact, in the introduction, the authors show two photographs of the same individual Paddyfield Pipit (*Anthus rufulus*) in different attitudes, just to make that very same point.

In short, *Pipits and Wagtails* is a monumental piece of scholarship, with a scope and attention to detail rarely found in such works; in fact, New World ornithologists will regret that it did not include the small number of pipits found in South America, which clearly need such a treatment. This book will undoubtedly be the definitive study of this charming group of birds for many years to come.—DAVID BREWER, Puslinch, Ontario, Canada; e-mail: mbrewer@albedo.net

## PROCEEDINGS OF THE EIGHTY-SIXTH ANNUAL MEETING

SARA R. MORRIS, SECRETARY

The eighty-sixth annual meeting of the Wilson Ornithological Society was held Thursday, 21 April, through Sunday, 24 April 2005, at the Sheraton Hotel in Beltsville, Maryland, in joint session with the Association of Field Ornithologists. The meeting was hosted by the U.S. Geological Survey (USGS) Patuxent Wildlife Research Center and the Maryland Ornithological Society, in cooperation with Friends of Patuxent, the U.S. Fish and Wildlife Service (USFWS) Patuxent National Wildlife Visitor Center, and the University of Maryland, Baltimore County. The Local Committee was co-chaired by Richard C. Banks and Jay M. Sheppard and included Nell Baldacchino, Roger B. Clapp, Alicia Craig, Deanna Dawson, Mercedes S. Foster, Mary Gustafson, Judd Howell, Joseph R. Jehl, Jr., Janet Millenson, Kevin Omland, Keith Pardieck, Bruce Peterjohn, Chandler S. Robbins, Jeff Spendelow, and Monica Tomosy. Additional assistance during the meeting was provided by Evelyn Adkins, Claudia Angle, Sarah Bennett, Kinard Boone, Fred Fallon, Regina Lanning, Jerry Persall, Luther Poellnitz, Fred Shaffer, Rachel Sturge, Marilyn Whitehead, and the Friends of Patuxent Volunteers. Alicia Craig organized and coordinated the electronic presentations for the paper sessions and Liz Humphries, Chris Hofmann, Beatrice Kondo, Spring Ligi, Anne Logie, and Bryan Rosensteel served as projectionists and technical support staff.

The Council met from 13:10 to 17:45 in the Severn Room and again from 20:30 to 21:57 in the Wye Salon on Thursday, 21 April, at the Sheraton Hotel. That evening there was an opening reception in the Susquehanna-Potomac Ballroom from 18:00 to 21:00.

Early morning field trips were led on Friday, 22 April, to Greenbelt National Park and Greenbelt by Dave Mozurkewich, Lake Artemesia–Greenbelt by Fred Shaffer, historical sights and sea duck facility of the Patuxent Wildlife Research Center by Matthew Perry, and the Whooping Crane breeding and reintroduction facility of the Patuxent Wildlife Research Center by Kathy O'Malley. On Saturday, 23 April, early morning trips included Lake Artemesia led by Fred Shaffer, the central tract of the Patuxent Wildlife Research Center led by Fred and Jane Fallon and Barbara Dowell, and a Jug Bay boat trip led by Greg Kearns. Post meeting trips on Sunday, 24 April, included Ft. Smallwood Park–Prince Georges County led by David Mozurkewich and Fred Fallon, the C & O Canal at Seneca/Sycamore Landing led by Jim Stasz and Ed Boyd, and a pelagic trip led by Mary Gustafson and Paul and Anita Guris.

On Friday, 22 April, Dick Banks, Co-chair of the Local Committee, welcomed guests to the Susquehanna-Potomac-Patuxent Room at the Sheraton Hotel. Dick Banks then introduced Judd Howe, Director of

the Patuxent Wildlife Research Center, who welcomed attendees and provided some of the ornithological history of the center, including its role as the home of the Breeding Bird Survey and the Bird Banding Laboratory. Gene Morton, President of the Association of Field Ornithologists, and Charles Blem, President of the Wilson Ornithological Society, welcomed attendees on behalf of the two societies. Jay Sheppard, Co-chair of the Local Committee, made several announcements about room changes, transportation for the poster session, and a request that students pick up their banquet tickets during the business meeting. Jim Rising, Chair of the Scientific Program, asked that attendees check the errata sheet for changes to the scientific program. Jed Burt provided background on Margaret Morse Nice and introduced Dr. Eugene S. Morton of Smithsonian Migratory Bird Center and Dr. Bridget J. M. Stutchbury of York University, who presented the ninth annual Margaret Morse Nice Plenary Lecture. Their lecture "Territoriality . . . Beyond the Temperate Zone" discussed territoriality, extra-pair paternity, and breeding synchrony in both the temperate and tropical zones in an attempt to break out of the temperate zone bias. Two concurrent paper sessions were presented in the Severn-Loch Raven Room and the Potomac-Susquehanna Rooms throughout the remainder of the scientific program. In addition to the Nice lecture, the scientific program included 76 contributed papers, organized into 10 paper sessions and 2 symposia—"Breeding Bird Survey" and "The Unselfish Gene: Honoring E. S. Morton's Contributions to Ornithology"—and 41 contributed posters.

The societies co-sponsored a student luncheon with "senior ornithologists" for 50 students at lunch on Friday. Friday evening, conferees attended the poster session and buffet reception at the Patuxent National Wildlife Refuge Visitors Center. Poster presenters were assigned to present their posters during half of the session, which provided additional room to view posters and fostered discussion.

On Saturday evening, a social hour preceded the annual banquet in the Ballroom of the Sheraton Hotel. After the dinner, Dick Banks thanked the local committee and all the individuals who had made the meeting a success. To present the Association of Field Ornithologists' awards, Gene Morton introduced Don Kroodsma, who presented the Bergstrom Awards, and Elissa Landre, who presented the Alexander Skutch Award. President Charles Blem briefly addressed the conferees, thanking Dick and Jay for hosting the meeting, the Local Committee for their service, and the Scientific Program Committee for a successful meeting. He thanked the retiring Members of Council for their service, welcomed the new Members of Council, and thanked all committee members for their hard

work. At that time the awards and commendations that follow were presented by Jed Burt (Margaret Morse Nice Medal), Charles Blem (Student Research Awards), Doris Watt (Student Presentation Awards), and Bob Curry (Commendations). The Student Travel Awards and Commendations for John Smallwood and Martha Vaughan were presented at the Business Meeting. The meeting was adjourned by acclamation at 20:58.

### MARGARET MORSE NICE MEDAL

(for the WOS plenary lecture)

Dr. Eugene S. Morton and Dr. Bridget J. M. Stutchbury, "Territoriality . . . Beyond the Temperate Zone."

### LOUIS AGASSIZ FUERTES AWARD

Joel W. McGlothlin, Indiana University, "Phenotypic integration of sexually selected traits in Dark-eyed Juncos (*Junco hyemalis*)."

### PAUL A. STEWART AWARDS

Julian Avery, Eastern New Mexico University, "The effects of habitat fragmentation on landscape-level processes and habitat associations of Nearctic-Neotropical migratory birds in New Mexico."

Aaron Ted Boone, Ohio State University, "Linking winter and migration events in a long-distance migratory songbird using stable-carbon isotope analysis."

Christy Anne Melhart, University of Arkansas, "Reproductive success and philopatry of Prairie Warblers, Blue-winged Warblers, Indigo Buntings, and Field Sparrows in declining scrub successional habitat in Connecticut."

Colin E. Studds, University of Maryland, "Linking non-breeding habitat occupancy to population processes in a Neotropical-Nearctic migratory bird."

### WILSON ORNITHOLOGICAL SOCIETY STUDENT TRAVEL AWARDS

Colleen Bell, Canisius College, "A crash course in communications tower mortality: birds dying to become a statistic in western New York."

Kristen M. Covino, Canisius College, "Getting to the point: rectrix shape morphometrics in age discrimination of Ovenbirds."

Michael F. Gaydos, Xavier University, "Factors affecting parental nest attendance in Northern Mockingbirds (*Mimus polyglottos*)."

George S. Hamaoui, Jr., Ohio Wesleyan University, "Analysis of feather-degradation by *Bacillus licheniformis* from the plumage of Botteri's Sparrows living in wet and dry habitats in Arizona."

Jennifer McNicoll, New Mexico State University, "Burrowing Owl nest site selection on the Janos-

Nuevo Casas Grandes, Mexico prairie dog complex."

Jennifer Newbrey, North Dakota State University, "Effects of nest contents and minimum daily temperature on female Yellow-headed Blackbird nest attentiveness."

Karan Odum, Ohio Wesleyan University, "Differences between vocalizations of wild-reared and human-reared birds of prey as an indication of learning within call development of owls and eagles."

Ashley M. Peele, Ohio Wesleyan University, "Feather damage in an albino Greater Frigatebird."

Jennifer Smolinski, Xavier University, "Numerical competence in wild Northern Mockingbirds (*Mimus polyglottos*)."

Rachel Sturge, University of Toronto, "The effects of habitat loss on the Savannah Sparrows (*Passerulus sandwichensis*) of La Perouse Bay, Manitoba."

Rebecca Suomala, University of New Hampshire, "Comparison of species distribution and habitat use during stopover on two islands in the Gulf of Maine."

Jennifer Urbanski, Canisius College, "Is shorter better? Does truncation increase the utility of open population models in stopover estimation?"

Kate E. Williamson, Ohio Wesleyan University, "The microbial ecology in the plumage of Neotropical migrants."

### ALEXANDER WILSON PRIZE

(for the best student paper)

Christopher Hofmann, University of Maryland-Baltimore County, "Pigment co-deposition and the masking of carotenoids in Orchard and Fuertes's orioles."

### LYNDS JONES PRIZE

(for the best student poster)

Beth A. Hahn, University of Michigan, "Using song playbacks to influence breeding habitat selection by American Redstarts."

Selection committee for the Nice Medal—William E. Davis, Jr. (Chair), Charles Blem, James Rising, and Doris Watt; for the Fuertes and Stewart Awards—Leann Blem (Chair), Charles Blem, Clait Braun, Dale Gawlik, Dale Kennedy, Dan Klem, David Podlesak, Craig Rudolph, and Doug White; for the Wilson Ornithological Society Travel Awards—Leann Blem (Chair); and for the Student Presentation Awards—Doris Watt (Chair), Alicia Craig, Bob Beason, Sandra Gaunt, and John Smallwood.

### COMMENDATION

WHEREAS John A. Smallwood accepted the challenge of moving from his role as Secretary of the Wilson Ornithological Society to assume the post of

Editor of *The Wilson Bulletin* at the start of the new millennium; and  
 WHEREAS he served as Editor for the years 2001–2003 and oversaw completion of volumes 113, 114, and 115; and  
 WHEREAS John approached his duties with diligent effort, hard work, and careful attention to the quality of the Society's premiere publication;  
 THEREFORE BE IT RESOLVED that the Wilson Ornithological Society thanks John Smallwood for his important and valuable service to the Society.

### COMMENDATION

WHEREAS Martha Vaughan served diligently as the Treasurer of the Wilson Ornithological Society over the past four years; and  
 RECOGNIZING that Martha brought to the position a degree of professionalism that has greatly increased the Society's ability to conduct operations, finances, and audits in a manner that fully reflects the organization's fiduciary responsibilities; and  
 RECOGNIZING that these improvements to the financial operations of the Society, by being instituted coincident with the doubling of the endowment through the William and Nancy Klamm bequest, represent an especially valuable contribution to the Society;  
 THEREFORE BE IT RESOLVED that the Wilson Ornithological Society expresses sincere gratitude to Martha for her important service to the Society.

### COMMENDATION

WHEREAS Charles R. Blem served the Wilson Ornithological Society as its President for the past two years with honor and distinction; and  
 RECOGNIZING that this service represents the continuation of many years of dedicated contributions to the Wilson Ornithological Society in many capacities; and  
 RECOGNIZING that under Charles's leadership, the Wilson Ornithological Society began evaluating its opportunities and responsibilities in light of receipt of the William and Nancy Klamm bequest, which increased the Society's endowment twofold; and  
 RECOGNIZING that during his term as President, the Wilson Ornithological Society has initiated a period of reinvigoration and new direction, as exemplified by changing the name of the *Bulletin* to the *Wilson Journal of Ornithology*;  
 THEREFORE BE IT RESOLVED that the Wilson Ornithological Society extends its thanks to Charles for his friendship and service to the Society.

### COMMENDATION

WHEREAS the Wilson Ornithological Society and the Association of Field Ornithologists jointly held their annual meetings in Beltsville, Maryland, with the sponsorship of the Patuxent Wildlife Research Center, USGS, and the Maryland Ornithological Society;

RECOGNIZING that the Friends of Patuxent, the National Wildlife Visitor Center of the USFWS, and the University of Maryland–Baltimore County made important contributions as meeting cooperators, facilitating the conduct of the scientific program, special events, and field trips; and  
 RECOGNIZING that attendance at the joint meeting was large and diverse, with notable involvement of graduate and undergraduate students as presenters and as volunteers, including especially the dedicated efforts of projectionists Liz Humphries, Chris Hofmann, Beatrice Kondo, and Spring Ligi; and  
 RECOGNIZING that the Chair of the Scientific Program Committee, Jim Rising, arranged a rich and extensive program of oral presentations, posters, and symposia; and  
 RECOGNIZING that the Committee on Local Arrangements, chaired by Dick Banks with assistance especially from Jay Sheppard and a host of others, organized and carried out an exciting and rich scientific conference;  
 THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and the Association of Field Ornithologists commend the Committee on Local Arrangements, the Scientific Program Committee, and all others who helped to make this meeting in Beltsville a great success and one that will be long remembered.

### BUSINESS MEETING

President Charles Blem called the business meeting to order at 13:09 in the Ballroom of the Sheraton Hotel–College Park. He thanked Dick Banks and Jay Sheppard for hosting the meeting and then introduced the members of the Wilson Council.

Secretary Sara Morris presented a summary of the Council meeting, which was held Thursday, 21 April. As of 15 April 2005, the Wilson membership stood at 1,848 including 172 students and 104 new members. We also have 555 institutional subscriptions to *The Wilson Bulletin*, 73 of which are new. As part of the Ornithological Societies of North America (OSNA) report, Council learned of several Wilson members who passed away during the last year, and Sara Morris asked those assembled to stand while she read the following names: William W. Baum (Cleveland Heights, OH), Frank C. Bellrose, Jr. (Havana, IL), John H. Dick (Meggett, SC), Thomas H. Foster (Bennington, VT), Frederick Greeley (Amherst, MA), Peter Hall (St. George's, Granada), William A. Jenner (Ofallon, IL), Ernst Mayr (Bedford, MA), Simon Rositzky (St. Joseph, MO), and Alexander Skutch (Costa Rica). After members were seated, Sara Morris announced that the Society received a generous bequest of \$1,000 from the estate of Thomas Foster.

During the last year, the management of the membership and executive director duties for OSNA were transferred from Allen Marketing and Management to the Schneider Group. The database transfer occurred in November, which resulted in late renewal announcements. A third renewal notice was sent to members to

help catch any lapsed memberships. OSNA now has a new Web site, [www.osnabirds.org](http://www.osnabirds.org), which is also the site of The Flock online.

Council thanked the Investing Trustees for their excellent work in managing the investments, and directed them to continue managing the Wilson portfolio for total return. Council approved the creation of three new awards. The William and Nancy Klamm Award will be given annually in recognition of significant contributions to the Society, beginning in 2006. Council also created the Nancy Klamm Award for the Best Undergraduate Oral Presentation and the Nancy Klamm Award for the Best Undergraduate Poster Presentation. Council increased the number of Stewart Research Awards from four to six per year. Council agreed to loan the North American Ornithological Conference (NAOC) organizing committee \$10,000 for seed money for the conference.

The Council reelected Jim Sedgwick as editor of *The Wilson Bulletin* for volume 118, with sincere gratitude for his work in getting *The Wilson Bulletin* back on its publication schedule. Now that the journal is back on schedule, Council voted for several changes to upgrade and modernize the Society's journal. Council voted to change the name of the journal from *The Wilson Bulletin* to *The Wilson Journal of Ornithology*. Council also approved changes to the cover of the journal, both in color and artwork. The Publications Committee will determine the exact artwork to use and the journal cover. These changes will be implemented in 2006, beginning with the first issue of volume 118.

Council heard updates on the preparations for the NAOC in Veracruz, Mexico next October. The Margaret Morse Nice Plenary lecture will open the NAOC next year.

Martha Vaughan presented the Treasurer's Report and Jim Sedgwick presented the Editor's Report. Leann Blem introduced the students receiving travel awards and Sara Morris presented banquet tickets to the students who were presenting papers at the meeting.

Jerry Jackson presented the report of the Nominating Committee, which included Charles Blem, Danny J. Ingold, Bette Jackson, and Doris Watt. 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, Sara R. Morris; Treasurer, Melinda M. Clark; and Members of Council (2005–2008), Kathleen G. Beal, Daniel Klem, Jr., and Douglas W. White. President Blem thanked the nominating committee and asked for any nominations from the floor. Hearing none, he accepted a motion to close nominations by Jay Sheppard, seconded by Ted Davis. John Kricher made the motion that the Secretary cast a single ballot for the slate of candidates, and Dick Banks seconded that motion. Secretary Morris cast the ballot, electing the officers and council members.

Dick Banks announced that 242 people had registered for the meeting.

Ernesto Ruelas Inzunza and Juan E. Martinez-Gómez gave a presentation that provided an overview of the plans for the fourth quadrennial North American Ornithological Conference in Veracruz City, Mexico, which is planned for 3–7 October 2006. The American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society, CIPAMEX, Raptor Research Foundation, Society of Canadian Ornithologists, Waterbird Society, and Wilson Ornithological Society will participate in the conference. The major venues are expected to be the World Trade Center and the Hotel Galeria and the initial projections expect 1,200 participants. They ended by encouraging everyone to attend the NAOC because, "We know how to have a good party."

Jerry Jackson gave a brief presentation on the history of the Association of Field Ornithologists and the Wilson Ornithological Society.

President Blem adjourned the meeting at 14:21 after a motion from John Kricher, which Jay Sheppard seconded.

## REPORT OF THE TREASURER

### OPERATING BUDGET FOR FISCAL YEAR 2005

Amended and Approved at Annual Meeting, 21 April 2005

	Actual 2004	Budget 2004	Budget 2005
<b>Operating Revenue</b>			
Direct Public Support (Contributions)	99	1,200	0
Memberships	38,552	46,000	46,000
Subscriptions	9,025	17,000	10,000
Page Charges	7,974	12,000	8,000
Royalties	1,086	1,600	1,000
BioOne Electronic Licensing	6,631	6,632	10,055
Sutton Fund—Transfer for Frontispieces	0	0	4,000
Sale of Back Issues & Books (Van Tyne Library)	465	1,000	0
<b>Total Operating Revenue</b>	<b>63,832</b>	<b>85,432</b>	<b>79,055</b>

**Operating Expenses**

Research Grants and Awards	6,000	6,000	6,500
Student Travel Grants	4,220	5,000	4,500
Van Tyne Library—Student Salaries/Benefits	0	2,000	3,000
Printing and Mailing Costs—Bulletin (Allen Press)	63,075	70,750	60,000
Editor's Honorarium, Contract, Expenses	55,878	55,595	55,000
OSNA Management Services	19,742	17,000	25,000
OSNA Executive Director	3,982	4,000	0
Storage Costs—Back Issues	1,761	2,000	2,000
Membership Development	0	1,500	0
Support—American Bird Conservancy	0	150	250
Support—Ornithological Council	10,000	9,000	9,000
Support—Ornithological Council Retreat	0	1,000	0
Tax Preparation Fees	525	525	580
Accounting Services	3,368	5,500	5,000
Insurance Expenses	1,166	1,150	1,200
General Expenses—Office, Postage, Copying, Bank Charges	347	1,000	1,000
Travel Expenses—Ornithological Council, OSNA, NABC, Annual Meetings	8,153	2,500	5,000
Annual Meeting 2005	0	0	5,152
Advance for 2006 NAOC Meeting	0	0	10,000
Nice Award Expenses	0	0	5,000
President's Discretionary Fund	0	0	4,000
Van Tyne Library Expenses	1,070	1,000	1,000
Award Costs	801	800	800
<b>Total Operating Expenses</b>	<b>180,088</b>	<b>186,470</b>	<b>203,982</b>
<b>Excess (Deficit)—Operating</b>	<b>(116,256)</b>	<b>(101,038)</b>	<b>(124,927)</b>
Total Investment Income (net of fees)	229,208	65,340	126,718
<b>Excess (Deficit) Including Investments</b>	<b>112,952</b>	<b>(35,698)</b>	<b>1,791</b>
Investment Bequest—Klamm Estate: Howland Capital Management	192,000	0	0
<b>Total Excess (Deficit) Including Klamm Bequest</b>	<b>304,952</b>	<b>(35,698)</b>	<b>1,791</b>

**STATEMENT OF ACTIVITIES**

FOR THE YEAR ENDING 31 DECEMBER 2004

**Change in Unrestricted Fund Balances****Revenues and Support**

Direct Public Support (Contributions)	\$	192,099
Memberships		38,552
Subscriptions		9,025
Page Charges		7,974
Royalties		1,086
BioOne Electronic Licensing		6,631
Sale of Back Issues & Books (Van Tyne Library)		465
Interest Income—Cash Accounts		0
<b>Total Revenues and Support</b>	<b>\$</b>	<b>255,832</b>

**Investment Income**

Realized Gains and Losses .....	\$	26,318
Unrealized Gains and Losses (change in market value) .....		134,976
Investment Earnings .....		69,827
<b>Total Investment Income .....</b>		<b>231,121</b>
<b>Total Revenues, Support, and Investment Income .....</b>	<b>\$</b>	<b>486,953</b>

**Expenses and Losses**

## Program Services

Research Grants and Awards .....	\$	6,000
Student Travel Grants .....		4,220
Award Costs .....		801
Van Tyne Library—Student Salaries/Benefits .....		0
Van Tyne Library Expenses .....		1,070
Printing and Mailing Costs—Bulletin (Allen Press) .....		61,075
Editorial Expenses .....		55,878
OSNA Management Services .....		19,742
OSNA Executive Director .....		3,982
Storage Costs—Back Issues .....		1,761
Support—Ornithological Council .....		10,000
<b>Total Program Services .....</b>	<b>\$</b>	<b>164,529</b>

## Supporting Services

Investment Fees .....	\$	14,346
Tax Preparation Fees .....		3,893
Insurance Expenses .....		1,166
General Expenses—Office, Postage, Copying, Bank Charges .....		347
Travel Expenses—Ornithological Council, OSNA, NABC, Annual Meetings .....		8,153
<b>Total Support Services .....</b>		<b>27,905</b>
<b>Total Expenses and Losses .....</b>	<b>\$</b>	<b>192,434</b>

**Total Change in Unrestricted Fund Balance**

		294,519
Unrestricted Fund Balance, Beginning .....		2,089,919
Unrestricted Fund Balance, Ending .....		2,384,438

**Change in Restricted Fund Balance (Sutton Fund)****Investment Income**

Unrealized Gains and Losses .....	\$	9,288
Investment Earnings .....		3,196
<b>Total Investment Income .....</b>	<b>\$</b>	<b>12,484</b>

**Expenses and Losses**

Investment Fees .....	\$	50
Transfer for Plate Fee .....		2,000
<b>Total Expenses and Losses .....</b>	<b>\$</b>	<b>2,050</b>

**Total Change in Restricted Fund Balance (Sutton Fund)**

	\$	10,434
Restricted Fund Balance, Beginning .....		129,510
Restricted Fund Balance, Ending .....		139,944

<b>Total Fund Balances .....</b>	<b>\$</b>	<b>2,524,382</b>
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## STATEMENT OF FINANCIAL POSITION

FOR THE YEAR ENDING 31 DECEMBER 2004

**Assets**

## Current Cash Assets

Operating Cash Accounts .....	\$	23,010
Cash Equivalents .....		24,530
Restricted Cash .....		2,060
<b>Total</b> .....	<b>\$</b>	<b>49,600</b>

## Investments

Equities .....	\$	2,036,027
Mutual Funds .....		26,648
Corporate Bonds .....		96,889
Fixed Income .....		315,218
<b>Total</b> .....	<b>\$</b>	<b>2,474,782</b>

<b>Total Assets</b> .....	<b>\$</b>	<b>2,524,382</b>
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**Fund Balances**

Unrestricted Fund Balances .....	\$	2,384,438
Restricted Fund Balances .....		139,944
<b>Total Fund Balances</b> .....	<b>\$</b>	<b>2,524,382</b>

Martha Vaughan, *Treasurer (ending 23 April 2005)*  
 Melinda Clark, *Treasurer (beginning 23 April 2005)*

**EDITOR'S REPORT—2004**

The Wilson Bulletin Editorial Office received 135 manuscripts during 2004 (vs 130 in 2003, 140 in 2002). All papers received three peer reviews, except in those rare instances when a referee failed to complete and return a review (<5% of cases). Correspondence from authors and referees was handled promptly (within 3 days of receipt). I accepted 28% and rejected 18% of manuscripts received in 2004, with the remainder (54%) having been returned to authors for extensive revision or revision and re-review. Volume 116 consisted of 39 major papers and 21 short communications; each issue had a color frontispiece. The mean time from receipt to publication for manuscripts published in volume 116 was 379 days, comparable with that of *Auk* (473 days) and *Condor* (320 days). The dates of publication for the issues of volume 116 were 6 August, 12 October, 10 December (2004), and 18 February (2005). Except for the original submission of manuscripts, most of the correspondence and document transmittal between the Wilson Bulletin Editorial Office and authors, reviewers, and Allen Press is now electronic.

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 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, copyediting, and consulting with Allen Press, frontispiece artists, and other editors. I thank Allen Press, and especially Karen Ridgway, for guidance and helpful advice on the final stages of the editorial and printing process. The USGS Fort Collins Science Center continues to be instrumental in its support of the editorial office. We welcome suggestions on how to improve the timeliness and quality of *The Wilson Bulletin*.

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 happened over the past calendar year with respect to the library:

**Loans:**

Loans of library materials to members included 44 transactions to 26 members. These loans included 4 books and 255 photocopied articles.

**Acquisitions:**

*Exchanges:* We received 136 publications by exchange from 113 organizations or individuals.

*Gifts:* We received 21 publications from 18 organizations.

*Subscriptions:* We also received 25 publications from 21 subscriptions. We spent \$768.30 on subscriptions in 2004.

*Donations:* Members, friends, and libraries donated 660 items. These donations included 78 books, 1 CD, 426 journal issues, and 155 reprints and reports.

*Donors:* The six members, friends, and libraries donating materials include E. H. Burt, C. Kersting, M. Lowther, M. Sogge, A. E. Staebler, and B. Weaver.

*Purchases:* New items purchased for \$200 included 11 books and 4 CDs of bird songs.

**Dispersals:**

*Gifts to other institutions:* A total of 33 journal issues were donated to Manuel Marin, Chile, and 21 journal issues to the Bonn Museum, Germany.

*Back issues:* We sent out 110 back issues of *The Wilson Bulletin* for only the cost of postage.

*Duplicates:* We sold 13 duplicate books and 61 duplicate journal issues for \$607: \$348 in cash, plus \$259 in credit from Buteo Books.

**Events:**

*Downsizing storage:* We moved part of our storage area for back issues of *The Wilson Bulletin* last summer. We anticipate moving the issues stored in the museum this summer and will probably reduce the number held.

We are making a concerted effort to fill in gaps in our journal holdings in anticipation of the Google Digitization Project. Every catalogued item in the University of Michigan Library will be scanned. All non-copyrighted items will be available to anyone online. Copyrighted items will be available to persons at the University, and through the WOS library, to WOS members. This will be a great project and should make ornithological literature available to researchers around the world.

**Accessibility on the Web:**

*Web site:* The Web site (<http://www.ummz.lsa.umich.edu/birds/wos.html>) continues to provide access to the library. Journals currently received are listed on the site as well as how to access the University of Michigan's online catalogue, which interested people can use to check holdings.

*Books for sale:* We have our duplicate books for sale listed on the Web site.

*Journals for trade:* Also listed on the Web are the journals we have available for sale or trade.

**Thank You:**

Many thanks to our secretary Janet Bell for keeping the library loan records and to our work-study student Erin Wiley for copying articles, keeping the library running, and mailing out back issues of *Wilson Bulletin*.

Janet Hinshaw, *Librarian*

**REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE**

This WOS Committee continues to maintain the Guide to Graduate Programs in Ornithology on the WOS Web site. I receive occasional e-mails from faculty at listed institutions requesting updates to their entries. From time to time, I receive e-mails from users who indicate the guide is a valuable resource for students contemplating graduate study in ornithology.

Herb Wilson, *Chair*

The Committee on the Scientific Program, chaired by James D. Rising, presented the following program of paper and poster sessions.

**PAPER SESSIONS**

David A. Aborn, University of Tennessee at Chattanooga, Chattanooga, TN, "The use of urban riparian forests by migratory landbirds."

Paul J. Baicich, Swarovski Birding and National Wildlife Refuge Association, Oxon Hill, MD, "A rice-and-bird synthesis: is it our 'next shade-grown coffee?'"

Susan L. Balenger, L. Scott Johnson, and Emilene Ostlund, Towson University, Towson, MD, "Does male UV-blue color indicate parental effort in Mountain Bluebirds?"

Jonathan Bart, USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, Boise, ID, "Sample size goals for monitoring North American nongame birds."

Robert C. Beason, Ohio Field Station, USDA Wildlife Services, National Wildlife Research Center, Sandusky, OH, "Avian vision and collision avoidance."

Colleen E. Bell, Sara R. Morris, Canisius College, Buffalo, NY; and Arthur R. Clark, Buffalo Museum of Science, Buffalo, NY, "A crash course in communications tower mortality: birds dying to become a statistic in western New York."

Steven R. Beissinger, Mark I. Cook, University of California, Berkeley, CA; Gary A. Toranzos, University of Puerto Rico, San Juan, PR; and Wayne J. Arendt, International Institute of Tropical Forestry, Luquillo PR, "Does incubation reduce microbial growth on eggshells and infection? . . . Why not!"

Peter V. Bradley, Nevada Department of Wildlife, Elko, NV; and Kenneth W. Voget, Ruby Valley, NV, "Winter night roost selection by Black and Gray-crowned rosy-finches in Northeast Nevada."

Jeffery J. Buler, Frank R. Moore, and Robert H. Diehl, The University of Southern Mississippi, Hattiesburg, MS, "Landscape-scale habitat use by landbirds during migratory stopover near an ecological barrier as revealed by weather radar and ground surveys."

Carolee Caffrey, Audubon Science, Ivyland, PA; Shauana S. C. Smith and Tiffany J. Weston, Oklahoma State University, Stillwater, OK; "West Nile Virus:

- pernicious effects on an American Crow population.”
- Paul Callo, Mary Baldwin College, Staunton, VA, “Survivorship and territory fidelity of Red-eyed Vireos (*Vireo olivaceus*).”
- B. T. Collins, Environment Canada, Canadian Wildlife Service, Ottawa, ON, Canada, “Optimizing sampling effort on remote routes.”
- Richard N. Conner, Clifford E. Shackelford, Richard R. Schaefer, and Daniel Saenz, USDA Forest Service, Southern Research Station, Nacogdoches, TX, “Fire suppression and Bachman’s Sparrows in pine forests of eastern Texas.”
- Kristen M. Covino, Joanna M. Panasiewicz, Sara R. Morris, and H. David Sheets, Canisius College, Buffalo, NY, “Getting to the point: rectrix shape morphometrics in age discrimination of Ovenbirds.”
- C. M. Downes, Environment Canada, Canadian Wildlife Service, Ottawa, ON, Canada, “The BBS in Canada.”
- H. I. Ellis, University of San Diego, San Diego, CA; and J. R. Jehl, Jr., Smithsonian Institution, Washington, DC, “Fat proportion of migrating and staging Eared Grebes does not differ.”
- William R. Evans, Old Bird, Inc., Ithaca, NY, “Broad-front migration + low cloud ceiling + hilly terrain = migration channeling.”
- Joelle L. Gehring, Central Michigan University, Mount Pleasant, MI; Paul Kerlinger, Curry & Kerlinger, LLC, Cape May Point, NJ; and Albert M. Manville, II, USFWS, Division of Migratory Bird Management, Arlington, VA, “Avian collisions with communication towers: a comparison of tower support systems and tower height categories.”
- Michael F. Gaydos and George L. Farnsworth, Xavier University, Cincinnati, OH, “Factors affecting parental nest attendance in Northern Mockingbirds (*Mimus polyglottos*).”
- Kirk M. Goolsby, Northern Virginia Community College, Annandale, VA, “Uneven energy savings in Canada Geese during formation flight: do birds exploit their position within the flock?”
- Russell Greenberg, Gregory Gough, and Daniel Boritt, Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC, “Neophobia in Mallards and other wild ducks.”
- George S. Hamaoui, Jr., and Edward H. Burt, Jr., Ohio Wesleyan University, Delaware, OH, “Analysis of feather-degradation by *Bacillus licheniformis* from the plumage of Botteri’s Sparrows living in wet and dry habitats in Arizona.”
- Kin-Lan Han, University of Maryland, College Park, MD; and Michael J. Braun, National Museum of Natural History, Smithsonian Institution, Suitland, MD, “Molecular phylogeny of Caprimulgidae (nightjars and nighthawks).”
- Gary H. Heinz and David J. Hoffman, USGS Patuxent Wildlife Research Center, Beltsville, MD, “The use of wild bird eggs to measure the sensitivity of avian embryos to methylmercury.”
- Christopher M. Hofmann, Thomas W. Cronin, Kevin E. Omland, University of Maryland–Baltimore County, Baltimore, MD; and Kevin J. McGraw, Arizona State University, Tempe, AZ, “Pigment co-deposition and the masking of carotenoids in Orchard and Fuetes’s orioles.”
- Rebecca L. Holberton, Jason C. Johnston, University of Maine, Orono, ME; and Peter P. Marra, Smithsonian Environmental Research Center, Edgewater, MD, “Habitats and hormones: understanding the physiological basis of life history stages in migratory birds.”
- C. Stuart Houston and Brenton Terry, Saskatoon, SK, Canada, “Turkey Vulture nestling travel, Saskatchewan to Costa Rica.”
- Austin L. Hughes and Helen Piontkivska, University of South Carolina, Columbia, SC, “DNA repeat arrays in chicken and human genomes and the adaptive evolution of avian genome size.”
- Cathie A. Hutcheson, Makanda IL; Leonard I. Wasenaar, National Water Research Institute, Environment Canada, Saskatoon, SK, Canada; and Lewellyn Hendrix, Southern Illinois University, Carbondale, IL, “Preliminary examination of the use of hydrogen isotope ratios in estimating the natal latitudes of hatch year Ruby-throated Hummingbirds.”
- Jerome A. Jackson, Florida Gulf Coast University, Ft. Myers, FL, “Art in science: the contributions of George Miksch Sutton.”
- Helen James, National Museum of Natural History, Smithsonian Institution, Washington, DC, “The biogeography and paleoecology of Koa-finches, extinct legume-eaters of the Hawaiian Islands.”
- L. Scott Johnson, Emilene Ostlind, and Susan L. Balenger, Towson University, Towson, MD, “Male parental effort at low and high elevations in a Wyoming population of Mountain Bluebirds.”
- Todd Katzner, Department of Conservation and Field Research, National Aviary, Allegheny Commons West, Pittsburgh, PA; E. J. Milner-Gulland, Imperial College London, Ascot, Berkshire, United Kingdom; and Evgeny A. Bragin, Naurzum National Nature Reserve, Kustanay Oblast, Naurzumskii Raijon, Dokuchaevka, Kazakhstan, “Using modeling to improve monitoring of birds: are we collecting the right data?”
- Paul Kerlinger, Curry & Kerlinger LLC, Cape May Point, NJ, “Appalachian ridge following by night migrating birds? A test of the hypothesis using marine surveillance radar in three states.”
- Daniel Klem, Jr., Muhlenberg College, Allentown, PA, “A humorous look at a deadly conservation issue: birds and glass.”
- Beatrice Kondo and Kevin E. Omland, University of Maryland–Baltimore County, Baltimore, MD, “Using New World orioles to address an old question: evolution of migration.”
- Lionel Leston and Amanda D. Rodewald, The Ohio State University, Columbus, OH, “Are urban forests ecological traps for birds?”
- James E. Lyons and Jaime A. Collazo, USGS Patuxent Wildlife Research Center and North Carolina Co-

- operative Research Unit, North Carolina State University, Raleigh, NC, "Plasma lipid metabolites and refueling performance at four stopovers along the migratory route of Semipalmated Sandpipers."
- Juan E. Martínez-Gómez, University of Missouri Saint Louis, Columbia, MO, and Island Endemics Foundation, Mexico, "Island conservation of Mexican insular avifaunas."
- Steven M. Matsuoka, Jim A. Johnson, U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK; Daniel R. Ruthrauff, Teresa L. Tibbitts, and Robert E. Gill, Jr., U.S. Geological Survey, Alaska Science Center, Anchorage, AK, "Estimating the global abundance of McKay's Buntings on St. Matthew Island, Alaska."
- Jennifer McNicoll, Martha Desmond, and Leigh Murray, New Mexico State University, Las Cruces, NM, "Burrowing Owl nest site selection on the Janos-Nuevo Casas Grandes, Mexico prairie dog complex."
- Alex Mills, University of Toronto, Toronto, ON, Canada, "Limits of ecomorphological analysis in explaining habitat specificity."
- Douglas Mock and P. L. Schwagmeyer, University of Oklahoma, Norman, OK, "Nestling begging and the problem of signal reliability."
- Jennifer L. Newbrey and Wendy L. Reed, North Dakota State University, Fargo, ND, "Effects of nest contents and minimum daily temperature on female Yellow-headed Blackbird nest attentiveness."
- Timothy O'Connell and Martin Piorowski, Oklahoma State University, Stillwater, OK, "Do wind turbines influence the density of breeding songbirds?"
- Karan J. Odom, Ohio Wesleyan University, Delaware, OH, "Differences between vocalizations of wild-reared and human-reared birds of prey as an indication of learning within call development of owls and eagles."
- Kevin E. Omland, University of Maryland-Baltimore County, Baltimore, MD, "Elaborate female coloration in tropical orioles (*Icterus*): phylogenetic and behavioral studies."
- Brent Ortego, Texas Parks and Wildlife Department, Victoria, TX, "Practical BBS sampling considerations when using volunteers."
- Harry W. Power, Rutgers University, New Brunswick, NJ; and Michael P. Lombardo, Grand Valley State University, Allendale, MI, "A graphical analysis of the costs of female copulatory activity in birds."
- John H. Rappole, Smithsonian Conservation and Research Center, Front Royal, VA, "Gene Morton's contributions to migratory bird ecology."
- Matthew W. Reudink and Robert L. Curry, Villanova University, Villanova, PA, "Extra-pair paternity and mate choice in a chickadee hybrid zone."
- Terrell D. Rich, U.S. Fish and Wildlife Service and Partners in Flight, Boise, ID, "Recommendations for rangewide population trend monitoring of North American landbirds."
- Chandler S. Robbins, USGS Patuxent Wildlife Research Center, Laurel, MD, "Reflections on 40 years of Breeding Bird Survey."
- J. A. Royle and J. R. Sauer, USGS Patuxent Wildlife Research Center, Laurel, MD, "Spatial coverage and inference: trade-offs between survey design and model assumptions in the North American Breeding Bird Survey."
- Ernesto Ruelas Inzunza, University of Missouri, Columbia, MO; Stephen W. Hoffman, Predator Conservation Alliance, Bozeman, MT; and Laurie J. Goodrich, Hawk Mountain Sanctuary Association, Kempton, PA, "Behavior of thermal soaring migrants in Veracruz, Mexico."
- John B. Sabine, Sara H. Schweitzer, University of Georgia, Athens, GA; and J. Michael Meyers, USGS Patuxent Wildlife Research Center, University of Georgia, Athens, GA, "Nest fate and productivity of beach nesting American Oystercatchers, Cumberland Island National Seashore, Georgia."
- John R. Sauer, William A. Link, James D. Nichols, and J. Andrew Royle, USGS Patuxent Wildlife Research Center, Laurel, MD, "The North American Breeding Bird Survey: credible, or not?"
- Richard R. Schaefer, D. Craig Rudolph, and Richard N. Conner, USDA Forest Service, Southern Research Station, Nacogdoches, TX, "Preliminary results from ongoing studies of nesting habitat, nestling provisioning, and foraging of the southeastern American Kestrel in the west Gulf Coastal Plain."
- Ralph W. Schreiber, Elizabeth A. Schreiber, National Museum of Natural History, Smithsonian Institution, Washington, DC; Ashley M. Peele, and Edward H. Burtt, Jr., Ohio Wesleyan University, Delaware, OH; "Feather damage in an albino Greater Frigatebird."
- Jay M. Sheppard, Laurel, MD; Kenneth P. Able, McArthur, CA; and Robin McCleery, Edward Grey Institute for Field Ornithology, South Parks Rd., Oxford, UK, "O.W.L. update."
- John A. Smallwood, Valerie Dudajek, Montclair State University, Montclair, NJ; Sivajini Gilchrist, Newark Museum, Newark, NJ; and Mary Anne Smallwood, Ironia School, Randolph, NJ, "Vocal development in American Kestrel (*Falco sparverius*) chicks: acoustical characteristics and ontogenetic patterns."
- Joseph Smith, Peter P. Marra, Smithsonian Environmental Research Center, Edgewater, MD; and Leonard R. Reitsma, Plymouth State University, Plymouth, NH, "Roosting behavior of the Northern Waterthrush during the non-breeding season."
- Jennifer L. Smolinski and George L. Farnsworth, Xavier University, Cincinnati, OH, "Numerical competence in wild Northern Mockingbirds (*Mimus polyglottos*)."
- Paul R. Spitzer, Cooperative Oxford Lab, Oxford, MD, "Ospreys a la Faaborg."
- Rachel Sturge, University of Toronto, Toronto, ON, Canada; and Robert Rockwell, American Museum of Natural History, New York City, NY, "The effects of habitat loss on the Savannah Sparrows (*Pas-*

- serculus sandwichensis*) of La Perouse Bay, Manitoba.”
- Rebecca Suomala, Kimberly Babbitt, University of New Hampshire, Durham, NH; and Sara Morris, Canisius College, Buffalo, NY, “Comparison of species distribution and habitat use during stopover on two islands in the Gulf of Maine.”
- Ethan J. Temeles, Robin S. Goldman, and Alexei U. Kudla, Amherst College, Amherst, MA, “Foraging and territorial economics of sexually-dimorphic Purple-throated Caribs, *Eulampis jugularis*, at three heliconias.”
- Monica Tomosy, USGS Patuxent Wildlife Research Center, Bird Banding Laboratory, Laurel, MD, “North American bird banding program review.”
- Jennifer M. Urbanski, Jerry Dudziak, Sara R. Morris, and H. David Sheets, Canisius College, Buffalo, NY, “Is shorter better? Does truncation increase the utility of open population models in stopover estimation?”
- Kate E. Williamson, University of Northern Colorado, Greeley, CO; and Edward H. Burt, Jr., Ohio Wesleyan University, Delaware, OH, “The microbial ecology in the plumage of Neotropical migrants.”
- Michael D. Wilson and Bryan D. Watts, College of William and Mary, Williamsburg, VA, “The influence of landscape configuration on the distribution and abundance of the Whip-poor-will (*Caprimulgus vociferus*).”
- Michael D. Wilson and Bryan D. Watts, College of William and Mary, Williamsburg, VA, “The influence of lunar conditions on the detection rate of the Whip-poor-will (*Caprimulgus vociferus*): implications for large-scale monitoring programs.”
- Petra Bohall Wood, USGS West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry, West Virginia University, Morgantown, WV, “Cerulean Warblers and canopy heterogeneity in West Virginia.”
- Bonnie E. Woolfenden, Bridget J. M. Stutchbury, York University, Toronto, ON, Canada; and Eugene S. Morton, National Zoological Park, Smithsonian Institution, Washington, DC, “Social isolation leads to a reduction in EP mating: is this a hidden cost of forest fragmentation?”
- Timothy F. Wright and Christine R. Dahlin, New Mexico State University, Las Cruces, NM, “The signal design of pair duets: does structure relate to function?”
- Tamaki Yuri, Michael J. Braun, National Museum of Natural History, Smithsonian Institution, Suitland, MD; Robert W. Jernigan, American University, Washington, DC; Robb T. Brumfield, Museum of Natural Science, Louisiana State University, Baton Rouge, LA; and Nirmal K. Bhagabati, The Institute for Genomic Research, Rockville, MD, “Different genetic markers reveal different levels of introgression in a *Manacus* hybrid zone.”
- TN; and Paul Hamel, USDA Forest Service, Center for Bottomland Hardwood Research, Stoneville, MS, “Breeding climate preferences of the Cerulean Warbler determined by spatial filtering of Breeding Bird Survey data.”
- Jacqueline Bennett and Gary Ritchison, Eastern Kentucky University, Richmond, KY, “Nest defense behavior of male and female Eastern Bluebirds.”
- Andrew J. Bernick, City University of New York-Graduate Center/College of Staten Island, Staten Island, NY, “Gull harassment and predation on adult Black-crowned Night-Herons in the New York City area.”
- M. J. Braun, C. J. Huddleston, K. L. Han, T. Yuri, J. Hunt, M. Krosby, Smithsonian Institution, National Museum of Natural History, Washington, DC; S. J. Hackett, J. Harshman, R. Bowie, S. Reddy, M. Burns, E. Sackett, R. Flynn, Field Museum of Natural History, Chicago, IL; E. Braun, R. Kimball, D. Steadman, J. Chojnowski, University of Florida, Gainesville, FL; W. Moore and K. Miglia, Wayne State University, Detroit, MI; F. Sheldon, B. Marks, C. Witt, Louisiana State University, Baton Rouge, LA; L. Christidis, J. Norman, Victoria Museum, Melbourne, Victoria, Australia; R. Page, University of Glasgow, Glasgow, Scotland, United Kingdom; R. T. Chesser, CSIRO, Victoria, Australia; and D. Swofford, Florida State University, Tallahassee, FL, “Early bird: a collaborative project to resolve the deep nodes of avian phylogeny.”
- W. P. Brown, P. Eggermont, V. LaRiccia, and R. R. Roth, University of Delaware, Newark, DE, “Can Wood Thrush growth be modeled using a non-parametric spline estimator?”
- Emily A. Caruana, Sarah M. Musilli, Michael S. Hurban, Canisius College, Buffalo, NY; Scott Weiden-saul, Ned Smith Center for Nature and Art, Millersburg, PA; H. David Sheets, and Sara R. Morris, Canisius College, Buffalo, NY; “Age-related differences in the fall migration of Northern Saw-whet Owls.”
- Kimberley Corwin, NYS Department of Environmental Conservation, Albany NY; and Kevin J. McGowan, Cornell Laboratory of Ornithology, Ithaca, NY, “New York’s second Breeding Bird Atlas.”
- Thomas Dietsch, Russell Greenberg, Peter Bichler, Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC; Ivette Perfecto, University of Michigan, Ann Arbor, MI; and Suzanne Langridge, University of California, Santa Cruz, CA, “Foraging ecology of migratory and resident birds in coffee agroecosystems of Chiapas, Mexico.”
- Matthew S. Dietz, University of Michigan, Ann Arbor, MI, “The effects of human and environmental stressors on White-crowned Sparrow corticosterone levels and reproductive success.”
- Walter G. Ellison, Maryland Ornithological Society, Chestertown, MD; and Mark Wimer, USGS Patuxent Wildlife Research Center, Laurel, MD, “Possible distributional changes detected by a second Breed-

## POSTERS

Jennifer Baldy, Esra Ozdenerol, Lensyl Urbano, Hsiang-te Kung, University of Memphis, Memphis.

- ing Bird Atlas in Maryland and the District of Columbia.”
- Kayde Gilbert, Janet Gorrell, and Gary Ritchison, Eastern Kentucky University, Richmond, KY, “Effects of West Nile Virus infection on the nest defense behavior of Eastern Bluebirds (*Sialia sialis*).”
- Beth A. Hahn, University of Michigan, Ann Arbor, MI, “Using song playbacks to influence breeding habitat selection by American Redstarts.”
- Marcy Heacker, Smithsonian Institution, National Museum of Natural History, Washington, DC; and Joe Witt, U.S. Fish and Wildlife Service, Potomac River National Wildlife Refuge Complex, Woodbridge, VA, “Osprey activity on the Potomac River.”
- Christopher M. Heckscher, University of Delaware, Newark, DE, “The Veery call repertoire: calls used in short- and long-distance communication in a migratory oscine passerine.”
- Elizabeth Humphries, Jeffrey L. Peters, Kevin E. Omland, University of Maryland–Baltimore County, Baltimore, MD; Jón E. Jónsson, and Alan D. Afton, USGS Louisiana Wildlife and Fisheries Cooperative Research Unit and School for Renewable Resources, Louisiana State University, Baton Rouge, LA, “Phylogenetics and phylogeography of the white goose complex, genus *Chen*: is Mother Goose spinning a new tale?”
- Michael S. Hurban, Emily A. Caruana, Sarah M. Musilli, Canisius College, Buffalo, NY; Scott Weidensaul, Ned Smith Center for Nature and Art, Millersburg, PA; H. David Sheets, and Sara R. Morris, Canisius College, Buffalo, NY; “Stopover rates and durations of migrant Northern Saw-whet Owls in southern Pennsylvania.”
- L. Scott Johnson, Brian S. Masters, Larry E. Wimmers, Bonnie G. Johnson, Robyn Milkie, Rachel Molinaro, and Brendan Gallagher, Towson University, Towson, MD, “Sex manipulation within broods of House Wrens? A repeat study.”
- Andrea Kraljevic, University of Michigan, Ann Arbor, MI, “The effects of ski slope fragmentation on avian diversity and behavior.”
- Patrick J. Kramer and James R. Hill, III, Purple Martin Conservation Association, Edinboro University of Pennsylvania, Edinboro, PA, “Locating and protecting Purple Martin roosts.”
- Sara A. Kuebbing, R. R. Roth, and J. L. Bowman, University of Delaware, Newark, DE, “Possible sexual dimorphism in breast spotting in the Wood Thrush and its potential for sexing.”
- Brook Lauro, St. John’s University, Jamaica, NY, “Habitat enhancement to improve waterbird productivity: what is the best method?”
- Jason Law and Emily Silverman, University of Michigan, Ann Arbor, MI, “Evaluating home range estimators for passerines.”
- Spring Ligi and Kevin Omland, University of Maryland–Baltimore County, Baltimore, MD, “Possible double brooding in temperate-breeding orioles: breeding behavior of Baltimore Orioles in Maryland.”
- Stephanie E. Little, Katherine E. Eggleston, Kristin Hnilicka, Bernard Lohr, and Douglas E. Gill, University of Maryland, College Park, MD, “Trill rate as a performance measure in Grasshopper Sparrow song.”
- Anne C. Logie, University of Maryland–Baltimore County, Baltimore, MD; Isabelle A. Bisson, Peter P. Marra, Smithsonian Environmental Research Center, Edgewater, MD; Patrick M. Gillevet, George Mason University, Manassas, VA; and Edward H. Burt, Jr., Ohio Wesleyan University, Delaware, OH, “A preliminary analysis of feather microbial communities on New World passerines.”
- Dana E. Long, R. R. Roth, and W. P. Brown, University of Delaware, Newark, DE, “Characteristics of repeat-pairs of Wood Thrushes: size, age, nesting characteristics and success.”
- Sarah Mabey, North Carolina State University, Raleigh, NC; Bryan Watts, Bart Paxton, Fletcher Smith, College of William and Mary, Williamsburg, VA; Barry Truitt, The Nature Conservancy, Virginia Coast Reserve Program, Nassawadox, VA; and Deanna Dawson, USGS Patuxent Wildlife Research Center, Laurel, MD, “Identifying stopover sites for migrating passerine birds in the lower Chesapeake Bay region.”
- Kathryn E. Mattern, Canisius College, Buffalo, NY; Rebecca W. Suomala, University of New Hampshire, Durham, NH; Melissa S. Mustillo, Peggy E. Buckley, Sara R. Morris, and H. David Sheets, Canisius College, Buffalo, NY; “Location, location, location: comparison of stopover at two sites.”
- Sarah M. Musilli, Michael S. Hurban, Emily A. Caruana, Canisius College, Buffalo, NY; Scott Weidensaul, Ned Smith Center for Nature and Art, Millersburg, PA; H. David Sheets, and Sara R. Morris, Canisius College, Buffalo, NY; “Sex-related differences in the migration of Northern Saw-whet Owls.”
- Melissa S. Mustillo, Elizabeth H. Lewis, Kathryn E. Mattern, Sara R. Morris, and H. David Sheets, Canisius College, Buffalo, NY, “Timing is everything: seasonal comparison of migratory stopover.”
- Emilene Ostlind, L. Scott Johnson, and Susan L. Balenger, Towson University, Towson, MD, “Egg and clutch size variation along an elevational gradient in Mountain Bluebirds.”
- Myra Shulman, Julie Ellis, Holly Jessop, Virginia Seng, and Katie Mach, Cornell University, Ithaca, NY, “Catastrophic effects from raccoon presence in gull breeding colonies.”
- Jeffrey A. Spendlow, USGS Patuxent Wildlife Research Center (PWRC), Laurel, MD; David A. Shealer, Loras College, Dubuque, IA; J. S. Hatfield, J. D. Nichols, PWRC; and I. C. T. Nisbet, I. C. T. Nisbet & Co., North Falmouth, MA, “Sex-specific survival rates of adult Roseate Terns: are males paying a higher reproductive cost than females?”
- Ian E. Tracy, Chris Hofmann, and Kevin E. Omland, University of Maryland–Baltimore County, Baltimore, MD, “Defining species limits through color: analysis of the Orchard Oriole complex.”

- Ursula Valdez, University of Washington, Seattle, WA, "Using aural surveys and radio-telemetry to determine the abundance and habitat use of forest-falcons in lowland Amazonian rainforest of southeast Peru."
- Lisa Vormwald, Roland Roth, Isis Johnson, and J. L. Bowman, University of Delaware, Newark, DE, "Inter-year distance between nest sites of Wood Thrush with respect to age, sex, previous year's success and mate's age."
- Doris J. Watt, Danelle Duffy, Leslie Kleczek, and Shannon Meyer, Saint Mary's College, Notre Dame, IN, "Comparisons of stress in House Finches using heterophil to lymphocyte ratios."
- Douglas W. White and E. Dale Kennedy, Biology Department, Albion College, Albion, MI, "Relation of season, clutch size, and egg order to hatching failure in House Wrens."
- Mark Wimer, Bruce Peterjohn, Anna Ott, and Naoko Griffin, USGS Patuxent Wildlife Research Center, Laurel, MD, "North American Breeding Bird Atlas viewer."
- Beth A. Wisotzkey and Roland Roth, University of Delaware, Newark, DE, "Survival of Brown-headed Cowbird and Wood Thrush eggs and young in Wood Thrush nests."
- Lindsay Zemba and Robert Curry, Villanova University, Villanova, PA, "Male dominance rank in an expanding hybrid zone between Black-capped Chickadees (*Poecile atricapillus*) and Carolina Chickadees (*P. carolinensis*) in southeastern Pennsylvania."

## ATTENDANCE

- ALASKA: *Anchorage*, Steve Matsuoka.
- ARIZONA: *Phoenix*, Troy Corman; *Tucson*, Clait E. Braun.
- ARKANSAS: *Fayetteville*, Douglas James.
- CALIFORNIA: *Berkeley*, Steve Beissinger; *San Diego*, Hugh Ellis.
- COLORADO: *Fort Collins*, Lori Nielsen, James A. Sedgwick; *Greeley*, Kate Williamson.
- DELAWARE: *Newark*, Bill Brown, Dana Long, Roland Roth, Lisa Vormwald, Beth Wisotzkey; *Smyrna*, Christopher Heckscher; *Wilmington*, Jean Woods.
- FLORIDA: *Fort Myers*, Jerome A. Jackson.
- GEORGIA: *Athens*, John Sabine; *Macon*, Todd Schneider; *Savannah*, Steven J. Wagner.
- IDAHO: *Boise*, Jon Bart, Terry Rich, Rex Sallabanks.
- ILLINOIS: *Makanta*, Cathie Hutcheson; *Springfield*, Vernon Kleen.
- INDIANA: *Indianapolis*, Alicia F. Craig; *Notre Dame*, Doris Watt; *South Bend*, Melinda Clark.
- IOWA: *Ames*, Bonnie Bowen.
- KENTUCKY: *Berea*, Jacqueline Bennett; *Frankfort*, Brainard Palmer-Ball, Jr.; *Richmond*, Kayde Gilbert, Gary Ritchison.
- MAINE: *Orono*, Rebecca Holberton.
- MARYLAND: *Annapolis*, Joseph R. Jehl, Jr.; *Arbutus*, Stephanie Little; *Baltimore*, Chris Hofmann, Elizabeth Humphries, Beatrice Kondo, Spring Ligi, Anne

- Logie, Kevin Omland, Bryan Rosensteel, Ian Tracy; *Beltsville*, Evelyn Adkins; *Chestertown*, Walter G. Ellison; *Chevy Chase*, Ellen Paul; *Clarksburg*, Jerry Persall; *College Park*, Bernard Lohr; *Edgewater*, Pete Marra, Joseph Smith; *Fort Washington*, Paul J. Baicich; *Greenbelt*, James A. Smith; *Largo*, Janet McMillen; *Laurel*, Deanna Dawson, Naoko Griffin, Mary Gustafson, Judd A. Howell, Marshall Howe, Kathy Klimkiewicz, James Lyons, Keith Pardieck, Bruce G. Peterjohn, Eleanor C. Robbins, Andy Royle, Jay Sheppard, Jeff Spindelov, Monica Tomosy, Mark Wimer, David Ziolkowski; *Silver Spring*, Greg Butcher, Adele Conover, Rob Hilton, Lisa Shannon; *Suitland*, Kirsten Braun, Michael Braun, Kin-Lan Han, Chris Huddleston, Tamaki Yuri; *Takoma Park*, Peter Blank; *Towson*, Susan L. Balenger, L. Scott Johnson; *Trappe*, Paul Spitzer.
- MASSACHUSETTS: *Amherst*, Donald Kroodsmas, Ethan J. Temeles; *Brookline*, Holly Jessop; *Chilmark*, Allan R. Keith; *East Falmouth*, William E. Davis, Jr.; *Hadley*, Randy Dettmers; *Marblehead*, Ann Bouchard; *Marshfield*, Andrea Jones; *Mattapoisett*, Elise Mock, George Mock; *Natick*, Elissa Landre; *Pocasset*, John Kricher, Martha Vaughan.
- MICHIGAN: *Albion*, Dale Kennedy, Doug White; *Ann Arbor*, Matthew Dietz, Beth Hahn, Andrea Kraljevic, Jason Law; *Chelsea*, Janet Hinshaw; *Farwell*, Joelle Gehring; *Kalamazoo*, Ray Adams.
- MINNESOTA: *Fort Snelling*, Tom Will.
- MISSISSIPPI: *Hattiesburg*, Jeffrey Buler; *Stoneville*, Paul B. Hamel.
- MISSOURI: *Columbia*, Ernesto Ruelas Inzunza; *St. Louis*, Juan E. Martínez Gómez.
- NEBRASKA: *Hastings*, Diane Beachly.
- NEVADA: *Elko*, Pete Bradley; *Las Vegas*, Cris Tomlinson.
- NEW HAMPSHIRE: *Center Harbor*, John P. Merrill; *Concord*, Pamela Hunt; *Epsom*, Rebecca Suomala.
- NEW JERSEY: *Cape May Point*, Paul Kerlinger; *North Plainfield*, Harry Power; *Randolph*, John A. Smallwood, Mary Anne Smallwood, Nathan Smallwood; *Somerset*, Bertram G. Murray, Jr.
- NEW MEXICO: *Albuquerque*, John Serles; *Las Cruces*, Jennifer McNicoll, Timothy F. Wright.
- NEW YORK: *Albany*, Kimberley Corwin; *Buffalo*, Colleen E. Bell, Peggy Buckley, Emily Caruana, Arthur R. Clark, Kristen Covino, Jerry A. Dudziak, Michael Hurban, Elizabeth Lewis, Katie Mattern, Sarah Musilli, Melissa Mustillo, Joanna Panasiwicz, H. David Sheets, Jennifer M. Urbanski; *Grand Island*, Elizabeth Morris, Sara Morris; *Ithaca*, William Evans; *Staten Island*, Andrew Bernick; *Utica*, Judy McIntyre, Pat McIntyre.
- NORTH CAROLINA: *Raleigh*, Becky Browning.
- NORTH DAKOTA: *Fargo*, Jennifer Newbrey, Michael Newbrey; *Sawyer*, Ron Martin.
- OHIO: *Cincinnati*, George Farnsworth, Michael Gaydos, Jennifer Smolinski, Sandra L. L. Gaunt, Lionel Leston; *Delaware*, Edward H. Burt, Jr., George S. Hamaoui, Jr., Chuck Jagger, Sarah A. Manor, Karan

- Odom, Ashley Peele, Vinod Saranathan; *Sandusky*, Bob Beason.
- OKLAHOMA: *Norman*, Douglas W. Mock; *Stillwater*, Tim O'Connell; *Tulsa*, Charles R. Brown, Mary Bomberger Brown.
- PENNSYLVANIA: *Allentown*, Daniel Klem, Jr.; *Cambridge Springs*, Eugene S. Morton; *Conneautville*, Joan Galli; *Edinboro*, James R. Hill, III, Patrick Kramer, John Tautin; *Ivyland*, Carolee Caffrey; *Montgomery*, Dana Brauning; *New Freedom*, Bruce G. Fortman; *Orangeville*, Douglas A. Gross; *Orwigsburg*, Rebekah Augustine, Keith L. Bildstein, Andres de la Cruz Munoz, Yelena Danilova, Gail Hall, Yedi Juarez Lopez, Sergio Seipke; *Palmyra*, Lindsay Zemba; *Philadelphia*, Wendy Lenhart; *Pittsburg*, Todd Katzner; *Scranton*, Michael Carey; *Villanova*, Bob Curry.
- RHODE ISLAND: *Narragansett*, Suzanne Lussier.
- SOUTH CAROLINA: *Columbia*, Austin Hughes.
- TENNESSEE: *Chattanooga*, David Aborn.
- TEXAS: *Lake Jackson*, Cecilia M. Riley; *Nacogdoches*, Richard N. Conner, Richard B. Schaefer; *Victoria*, Brent Ortego.
- WASHINGTON, DC: Claudia Angle, Tom Bancroft, Roger Clapp, Thomas Dietsch, Robert Fleischer, Mercedes S. Foster, Russell Greenberg, Helen James, Chris Milensky.
- VERMONT: *Northfield*, William Barnard.
- VIRGINIA: *Alexandria*, Richard C. Banks, Betty Anne Schreiber; *Annandale*, Walter Bulmer; *Fairfax*, Marcy Heacker; *Front Royal*, John Rappole; *Lynchburg*, Gene Sattler; *Portsmouth*, Elisa Enders; *Richmond*, Charles R. Blem, Leann Blem, Sergio Harding, Mike Wilson; *Shipman*, Allen Hale; *Staunton*, Paul A. Callo; *Warrenton*, Kirk M. Goolsby.
- WASHINGTON: *Bainbridge Island*, Lee Robinson; *Seattle*, Ursula Valdez.
- WEST VIRGINIA: *Bethany*, Albert R. Buckelew, Susan Buckelew; *Millstone*, Thomas R. Fox; *Montgomery*, Deborah Beutler; *Morgantown*, Petra Wood.
- CANADA
- ALBERTA: *Edmonton*, Brenda Dale.
- BRITISH COLUMBIA: *Naramata*, Dick Cannings.
- NEW BRUNSWICK: *Sackville*, Dan Busby.
- ONTARIO: *Mississauga*, Rachel Sturge; *Newmarket*, Kimberly Jones; *Ottawa*, Brian Collins, Constance Downes, Erica Dunn, Charles M. Francis, Bev McBride; *Toronto*, Ioana Chiver, Melissa Evans, Alex Mills, Levi Moore, James Rising, Bridget Stutchbury, Bonnie Woolfenden.
- QUÉBEC: *Sainte-Foy*, Gilles Falardeau.
- SASKATCHEWAN: *Saskatoon*, Mary Houston, Stuart Houston, Alan R. Smith.

## REVIEWERS FOR VOLUME 117

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 graciously served as referees for this volume of *The Wilson Bulletin* (referees who contributed two or more reviews appear in boldface). The Wilson Ornithological Society and the editorial staff of *The Wilson Bulletin* are deeply grateful to them for their assessments and recommendations.—James A. Sedgwick, Editor.

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By Kathleen G. Beal

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